The Impact of Edge Effects & Matrix Restoration on Dung Beetle Community Structure & Ecosystem Function

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ABSTRACT

Land-use change has become a force of global importance and has gained status as the most important driver of ecosystem degradation. The resulting creation of habitat edges has pervasive impacts on the distribution and persistence of species in forest ecosystems. Responses of species to edge effects can be highly dependent on ‘response’ traits, which may in turn co-vary with ‘effect’ traits that determine rates of ecosystem functioning. Therefore, non-random loss of species due to traits conferring higher susceptibility to extinction may also result in the loss of functionally-important species across a habitat edge gradient. Likewise, response and effect traits may be important in determining reassembly of communities in regenerating habitats, which may provide insight into potential scenarios of functional responses to restoration efforts. To test for potential off-site effects of adjacent matrix habitat restoration on dung beetle communities, I compared dung beetle community structure and species trait composition across Afromontane forest edges adjacent to degraded and regenerating matrix habitat at Ngel Nyaki forest reserve in Nigeria. I also measured dung removal rates across habitat edge gradients to investigate the relative off-site impacts of matrix restoration on dung beetle-mediated ecosystem processes. I found significant effects of adjacent matrix condition on edge response functions in dung beetle abundance, species distributions, and trait composition. Beetle abundances were markedly higher in forests adjacent to regenerating matrix, whereas the largest differences in trait composition were found between degraded and regenerating matrix habitat, indicating the presence of ecological filtering processes in these areas. Furthermore, I found that species traits determined community structural responses to environmental change and this had strong flow-on effects to rates of dung removal. Shifts in trait distributions explained dung removal rates above and beyond total beetle mass, suggesting that neutral processes alone could not explain functional efficiency. In particular, habitat regeneration resulted in the assembly of communities with high total beetle mass and on-average smaller beetles, which was optimal for functional efficiency. In conclusion, the restoration of adjacent matrix habitat was shown to effectively mitigate edge effects on dung beetle community structure resulting in the re-establishment of important associated ecosystem processes.

Chapter 1: Introduction

Land-use change is the single largest driver of biodiversity loss worldwide (Sala et al. 2000, Foley et al. 2005). Habitat destruction and the subsequent fragmentation and isolation of remaining habitat patches have led to a substantial decline in biodiversity, while further threats to remaining populations within these remnant habitats have been exacerbated by intensification of land use in the surrounding production matrix. These processes have varying and profound effects on species diversity, community structure, and resilience of these communities to further disturbances (Saunders et al. 1991, Turner 1996, Fahrig 2003, Strayer et al. 2003).

Fragmentation of natural ecosystems typically results in the alteration of five major factors that drive community responses: a decrease in average patch size, an average increase in patch isolation and patch shape complexity, and an average increase in matrix contrast and edge influence (Ewers and Didham 2006a). These proximate drivers of fragmentation effects can have wide-ranging impacts on biotic and abiotic variables. For example, with decreasing habitat size, a decrease in species richness is often observed (Dennis et al. 1998, Ricklefs and Irby 1999, Flaspohler et al. 2010). Furthermore, a recent study by Struebig et al. (2011) found that with fragment-area driven declines in species richness, there is also a correlated loss in population level genetic diversity. However, the relationship between habitat area and species richness can be highly variable due to other interacting factors, such as variation in the surrounding matrix structure and the invasibility of the habitat patch by exotic species (Jablonski 1996, Davies et al. 2004). Patch isolation can be altered through various factors such as changes in matrix structure or the distance between habitat patches. This can have severe impacts on species persistence as it can reduce the probability and rate of dispersal between patches (Ostfeld and LoGiudice 2003, Ewers and Didham 2006a), potentially increasing inbreeding depression in isolated populations and increasing dispersal-related mortality (Kremen 2005, Baker and Barmuta 2006). Additionally, through the production of multiple smaller habitat patches and the alteration of patch shape, these processes can increase the proportion of edge habitat in remnant patches. As a result, edge effects are more likely to negatively affect a larger proportion of habitat area in a fragmented landscape (Saunders et al. 1991, Fagan et al. 1999, Laurance et al. 2002).

Particularly strong responses to habitat fragmentation have been demonstrated for invertebrate communities (Klein 1989, Didham et al. 1998, Laurance et al. 2002). This has been shown to have significant ecological, as well as economic, flow-on effects due to impacts on important ecosystem services provided by invertebrates, such as nutrient cycling and pollination (Didham et al. 1996, Kearns et al. 1998, Cane and Tepedino 2001, Kremen et al. 2007). More recently, invertebrate communities have been used to demonstrate the pervasive effects of habitat edges in fragmented landscapes but these effects have rarely been explicitly related to impacts on ecosystem functioning across forest edges (Ewers and Didham 2008). Further studies on invertebrate and bird communities have elucidated the potential interaction between edge effects and other fragmentation factors, such as habitat area, providing evidence that edge effects may in fact be the major underlying driver of fragmentation-related ecosystem responses (Ewers et al. 2007, Banks-Leite et al. 2010).

1.1 Ecosystem responses to human-induced habitat edges

Since the early 1930’s, it has been recognised that there are changes in ecosystem structure around habitat edges. Leopold (1933) noted that, at habitat edges, there appear to be increases in abundances of various species, and thus suggested implementing the production of habitat edges as a means of increasing numbers of game species. However, since the early views of Leopold, there has been the realisation that habitat edges predominantly result in the degradation of natural ecosystems (Laurance et al. 2002, Harper et al. 2005). The creation of edges through forest fragmentation initially alters vegetation structure. This process results in immediate changes in microclimatic factors such as increases in wind disturbance, solar radiation, evapotranspiration, temperature stochasticity, and a decrease in soil and atmospheric moisture (Murcia 1995, Chen et al. 1999, Laurance et al. 2011). These changes induce relatively rapid responses in plant communities, with an increase in pioneer species, understory density, and thinning of the upper canopy (Murcia 1995, Gascon et al. 2000, Laurance et al. 2002, Harper et al. 2005). As overall vegetative structure changes, this leads to major shifts in associated invertebrate communities, which are also directly affected by the microclimatic changes near the forest edge (Didham et al. 1998). These proximate responses are often the most conspicuous, but there are potential indirect effects which may be far-reaching and especially insidious, such as the alteration of species interactions (Fagan et al. 1999, Ewers and Didham 2006a) and loss of ecosystem function (Didham 1998, Chen et al. 1999). Changes in species interactions and functional provisioning can result in negative feedbacks, leading to an increased rate of decay of the ecological integrity of natural remnants (Jones et al. 1997, Wu et al. 2011).

Edge effects are continuous processes that occur as gradients of change across a habitat boundary. Therefore, to understand the impact that edge effects have on habitat remnants, they must be quantified as a single continuous response function encompassing both sides of the habitat boundary. By measuring on continuous scales, this gives the ability to generate response functions that can indicate the extent to which these effects penetrate into habitat remnants and the magnitude of change in species responses (Ewers and Didham 2006b). Quantifying edge effects in a spatially explicit manner can provide insight into the relative impact that edge effects pose on remnant habitats (Ewers and Didham 2006b). It also provides a platform to test how interacting drivers may alter the impact of edge effects as the extent and magnitude of edge influence depends on edge structure, matrix structure, and adjacent land use intensity (Didham and Lawton 1999, Haynes and Cronin 2006, Piessens et al. 2006).

1.2 The effects of land-use intensity on remnant ecosystems

The effects of adjacent matrix structure on natural habitat patches are demonstrated clearly in studies measuring edge effects and community responses to habitat edges. There is already a wealth of studies that elucidate the significant influence of habitat edges in remnant ecosystems (Harper et al. 2005). Many of these studies clearly make the assumption that patterns in community structure near habitat edges are in fact a product of the relationship between the structure of the matrix and the remnant habitat (Murcia 1995, Strayer et al. 2003). However, relatively few studies have explicitly measured the degree of dependence of edge responses on adjacent matrix structure, especially within the context of varying land-use intensity in the adjacent habitat (but see Piessens et al. 2006, Pawson et al. 2008).

With the rapid increase in human population, there are strong socioeconomic drivers for the intensification of agricultural production to cater for a growing global food demand (Tilman et al. 2001). This has led to a rapid increase in the intensity of agricultural and rangeland practices, which appear to be especially significant and destructive in developing regions of the world (Tinker 1997, Lambin et al. 2003). Land-use intensification can have widespread impacts on ecosystems through the alteration of biogeochemical processes and changes in plant communities (DeFries et al. 2004), which in turn can have profound impacts on associated invertebrate communities (Jones et al. 2003, Attwood et al. 2008).

In particular, livestock grazing can significantly alter ecosystem structure through factors such as trampling, nutrient enrichment of soils, and selective browsing. Trampling by livestock causes soil compaction which can significantly alter nutrient levels in the soil, increase soil erosion, and alter soil microbial communities (Martinez and Zinck 2004, Pietola et al. 2005). Additionally, trampling from livestock can have severe impacts on plant biomass, resulting in the loss of above-ground carbon stocks and alteration of the three-dimensional structure of vegetative cover (Reid and Hochuli 2007). In turn, this can render these communities more vulnerable to biological invasions by more ‘trampling-resistant’ species of plants, which can out-compete native species, potentially altering the entire structure of plant communities (Hobbs and Huenneke 1992). Such a community-wide shift in vegetative structure, this can lead to a shift in associated invertebrate communities (Dennis et al. 1998, Siemann et al. 1998, Reid and Hochuli 2007). Furthermore, livestock grazing can drive a shift in plant community composition towards low-diversity assemblages, resulting in a decrease in habitat heterogeneity which can significantly decrease invertebrate species richness and alter plant-insect interactions (Kruess and Tscharntke 2002).

Land-use intensification clearly imposes severe on-site effects (where the land use is occurring), which drive community responses and alter ecosystem processes. What is less well appreciated is that land-use intensification can also have substantial off-site effects (i.e. effects that spill-over into the wider landscape). A handful of studies have elucidated the potential impact of the surrounding land-use matrix structure on within-fragment ecosystem dynamics (Denyer et al. 2006, Laurance et al. 2011). These studies suggest that in order to fully grasp the magnitude of influence that the adjacent matrix has on remnant ecosystems, it is imperative we take into account the structural characteristics and degree of degradation of the surrounding matrix. Adopting a perspective wherein habitat remnants and adjacent matrix are ecologically coupled provides a more cohesive functional framework for fragmentation studies that extend from within-patch dynamics to a landscape scale (Kupfer et al. 2006). Given the relative importance of edge effects in fragmented landscapes, along with the rapid rate of land-use intensification worldwide (Tilman et al. 2001), this highlights the need to better quantify these interacting drivers in order to understand ecological responses to anthropogenic land-use change.

1.3 Do trait differences determine species' responses and ecosystem function?

The integration of multiple drivers of biodiversity loss in empirical research provides a mechanistic understanding of responses to habitat fragmentation. However, in studies attempting to quantify community responses to anthropogenic disturbance, another cause of uncertainty often stems from highly variable responses among species that can lead to spurious conclusions if this variability is overlooked (Ewers and Didham 2006a). Therefore, a fully integrative approach that identifies the variability of species responses to multiple interacting drivers is required to accurately predict ecosystem responses under various global change scenarios.

Species responses to environmental change are highly variable due to differences in morphological and life-history traits conferring different levels of susceptibility to disturbances (Davies et al. 2004, Henle et al. 2004, Ewers and Didham 2006a). The main traits that determine different levels of extinction proneness in species include body size, dispersal ability, rarity, trophic level and niche breadth (Ewers and Didham 2006a). All of these traits interact with each other and with various anthropogenic drivers differently, resulting in complex responses of communities to these drivers (Ewers and Didham 2006a). With an understanding of these trait-mediated responses and how they interact, we can gain a better mechanistic understanding of how species assemblages respond to global change drivers. For example, it is often assumed that larger-bodied organisms will be more sensitive to habitat loss and fragmentation due to the need for larger habitat area, larger resource requirements, and lower reproductive rates (Jablonski 1996, Bennett and Owens 1997). Additionally, dispersal ability is often positively correlated with species persistence in fragmented landscapes (Driscoll and Weir 2005). This is because these species are more likely to maintain inter-patch dispersal, thus increasing chances of resource acquisition in degraded landscapes and maintaining inter-population genetic exchange (Tscharntke et al. 2002, Meyer and Kalko 2008). However, the dispersal-sensitivity relationship may invert depending on the landscape context, whereby farther dispersing species become more likely to leave pristine habitat and experience higher mortality rates in the hostile matrix, acting as an ecological sink (Ewers and Didham 2006a).

While traits exhibited by species determine their persistence and distribution, these traits also determine how species perform in an ecosystem. In other words, variation in particular species traits might mediate ecosystem processes to differing degrees. These traits are known as ‘functional effect traits’ (Lavorel and Garnier 2002, McGill et al. 2006, Webb et al. 2010). For example, many plant traits have been identified as important functional effect traits, such as specific leaf area, leaf nitrogen content, and relative growth rate, as these all have significant impacts on nutrient inputs and uptake (Garnier et al. 2004, Orwin et al. 2010). Additionally, body size of invertebrates is often implied to be an important functional effect trait as it scales closely with resource uptake (de Bello et al. 2010, Lecerf and Richardson 2011) As these traits affect external processes in the surrounding ecosystem, it is important that they are measured to understand the functional consequences of individual species losses (Webb et al. 2010).

Furthermore, there may be potential correlations between ‘response traits’ (traits determining species’ sensitivity to disturbances) and ‘effect traits’ (functional traits) within species (Lavorel and Garnier 2002, Larsen et al. 2005). If these traits are negatively correlated, this would mean that while a species may exhibit a trait that makes it highly sensitive to disturbance, this could be of little importance in a functional sense because the trait confers a lower functional significance for the process in question. However, in the case of a positive correlation between response and effect traits, this would imply that a trait conferring higher sensitivity would also impart greater functional importance. For example, Larsen et al. (2005) found that with increasing body size in bumble bees, species were both more extinction prone but also provided greater levels of pollination. This was due to the positive correlation between body size and dispersal ability which increased the bumblebees ability to pollinate over larger distances. If this response-effect trait relationship occurs, this results in a non-linear rate of ecosystem function loss in response to anthropogenic disturbance. Potentially, there may be exponential losses of ecosystem function with species extinctions, resulting in the rapid degradation of natural systems and ecosystem services (Ostfeld and LoGiudice 2003, Kremen 2005). This exemplifies the importance of identifying relationships between species responses in order to better understand trajectories in the structuring of communities and resulting ecosystem processes in the face of global environmental change.

1.4 Dung beetles as a focal taxon for habitat fragmentation studies

Dung beetles (Coleoptera: Scarabaeinae) are a suitable ecological indicator for studies investigating responses of communities to anthropogenic land use change as they are highly responsive to minor environmental changes, easy to sample, highly diverse and abundant, and mediate important ecosystem processes (Favila and Halffter 1997, Davis et al. 2001, McGeoch et al. 2002, Larsen et al. 2008, Verdú et al. 2011). Additionally, due to their important role in dung removal and a very high level of variation in morphological traits, this taxonomic group is ideal for trait-based ecological research attempting to investigate functional effects of anthropogenic land-use change (Larsen et al. 2005, Larsen et al. 2008).

Dung beetles are a cosmopolitan group of beetles found on every continent except Antarctica and they inhabit a vast range of ecological niches (Hanski and Cambefort 1991). They are particularly abundant and diverse in the tropics, where they are responsible for a significant proportion of dung and carrion decomposition (Nichols et al. 2008). As adults, Scarabaeine dung beetles utilise dung as a resource for food, but more importantly as a resource for rearing larvae. Adult dung beetles fly to a fresh dung pat and immediately excavate tunnels, either directly under or laterally away from the dung pat. The beetles then lay eggs in brood balls of dung which are taken into the tunnels where the larvae will develop and eat the dung which the parent (or parents) have provisioned (Hanski and Cambefort 1991).

Due to their life-history characteristics, Scarabaeine dung beetles are important for nutrient cycling processes and secondary seed dispersal in tropical ecosystems. For example, as dung is taken apart into smaller quantities and further broken down by the larvae, this process increases microbial action. In turn, the rate of nitrogen mineralisation is increased, which reduces the loss of N through ammonia volatilisation (Yokoyama et al. 1991), thereby increasing levels of available labile N in the soil (Nichols et al. 2008). Furthermore, when dung beetles excavate tunnels for burying brood balls, the bioturbation of the soil increases oxygen levels throughout the upper soil horizon which then increases aerobic bacterial action and further enhances decomposition rates (Yokoyama et al. 1991, Nichols et al. 2008). In addition to increasing rates of nutrient cycling, which enhances soil quality for plant growth (Wu et al. 2011), dung beetles also provide secondary dispersal of plant seeds (Nichols et al. 2008). This process occurs when seeds that have been ingested and then defecated out by frugivores are inadvertently removed and buried as dung beetles are excavating tunnels for their brood balls (Vander Wall et al. 2005). As secondary seed dispersal by dung beetles deposits seeds just under the soil surface, this process decreases seed predation rates and facilitates germination and seedling establishment (Shepherd and Chapman 1998, Andresen 2002). Through these processes, dung beetles play a key role in maintaining processes which contribute to shaping the structure of ecosystems.

Dung beetles have been used as focal taxa in many studies for the quantification of community responses to anthropogenic disturbances, especially habitat fragmentation (Nichols et al. 2007). In particular, this group has shown strong changes in diversity, abundance, and overall community disassembly in response to fragmentation (Klein 1989, Larsen et al. 2008, Davis and Philips 2009, Filgueiras et al. 2011). The degree of such responses has also shown high interdependence with matrix structure and land-use intensification adjacent to the focal habitat (Davis et al. 2000, Hutton and Giller 2003, Díaz et al. 2010). Surprisingly, despite the vast body of literature on dung beetle responses to habitat fragmentation and also a number of studies that focus on their responses to human land-use intensification, there have been no studies to date that investigate the interaction between land-use intensification and edge effects on dung beetle communities (Nichols et al. 2007). Furthermore, while there have been a number of studies that have sampled at discrete edge, interior, and matrix points (Davis et al. 2000, Spector and Ayzama 2003), almost no studies have sampled across continuous forest-to-edge response gradients (but see Duraes et al. 2005). While previous studies provide some evidence that dung beetles respond to habitat edges, there is still little spatially explicit knowledge of how this taxa responds and what the overarching consequences may be for community composition and ecosystem processes. This gap in knowledge requires urgent attention, given that edge effects have been implicated as one of the most important drivers of ecosystem degradation related to habitat fragmentation (Ewers et al. 2007, Banks-Leite et al. 2010, Laurance et al. 2011)

The functional consequences of dung beetle species loss and decreases in abundance can be far reaching, with potentially large losses in nutrient cycling and secondary seed dispersal that can have dramatic effects on entire plant communities (Andresen 2003, Slade et al. 2007, Slade et al. 2011, Wu et al. 2011). Furthermore, studies have suggested the importance of dung beetle species traits, such as body size and dispersal ability, in determining responses to anthropogenic disturbances (Driscoll and Weir 2005, Larsen et al. 2008). It has also been found that traits, such as body size, are strongly correlated with functional importance of dung beetle species (Klein 1989, Larsen et al. 2005, Nichols et al. 2008). However, until recently there has been little investigation into the relationship between these response and effect traits for invertebrates, and specifically in dung beetles, despite the potential correlations between such traits for these taxa (Larsen et al. 2005).

1.5 Mitigating edge effects in an Afromontane forest through matrix restoration

The overall aim of this study is to quantify the relative impact of restoring the adjacent matrix habitat on the intensity of edge effects at human induced forest-to-matrix edge gradients. Building on a vast wealth of previous empirical evidence for the proximate effects of habitat edges on ecosystems, I focus on community edge responses of dung beetles under the mediating effects of adjacent matrix restoration and the resulting rates of dung removal. This is represented in Figure 1.1 by the top pathway, where I also include hypothetical outcomes for plant and microbial communities and resulting feedbacks of ‘effect’ processes on community responses. I quantify these impacts in a Nigerian Afromontane forest system using a response-effect trait framework, which provides a mechanistic elucidation of the determinants of species responses and, importantly, demonstrates how these drivers of environmental change can have cascading impacts on ecosystem processes.

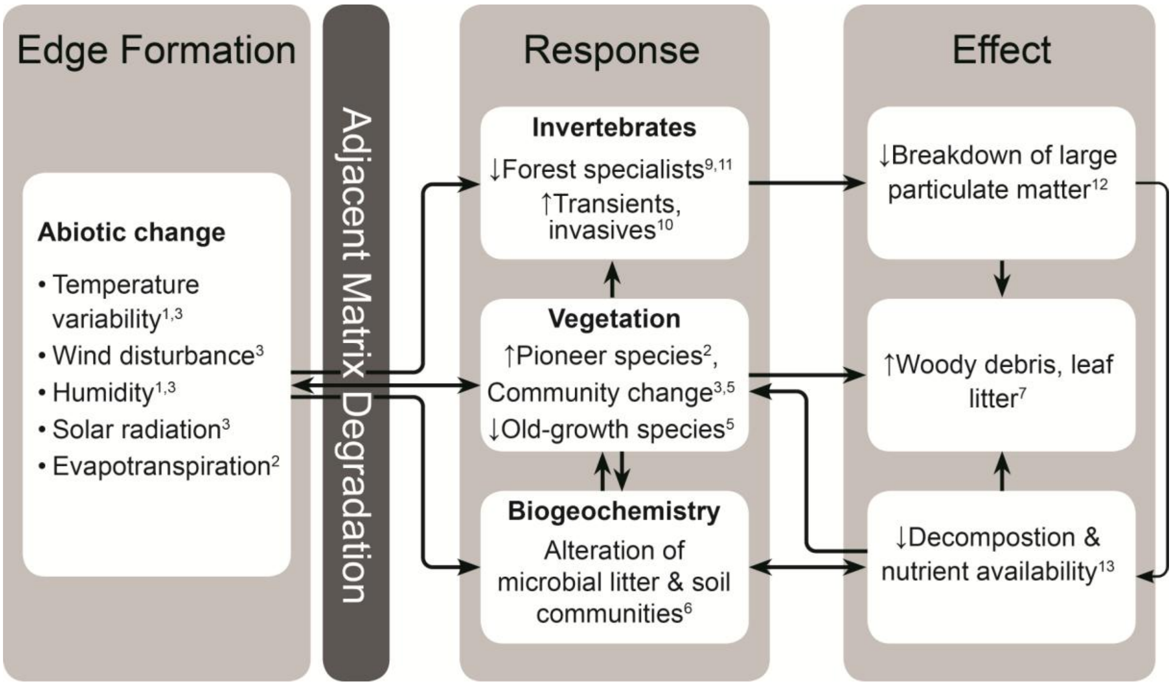


Figure 1.1 Conceptual framework for the progression from community responses to ecosystem effects in plant, invertebrate, and microbial communities as a result of habitat edge formation and interaction with adjacent matrix degradation. ↑ and ↓ indicate an increase or decrease of a factor respectively. Arrows between boxes indicate the direction of influence. The Edge Formation phase refers to the process of habitat loss and edge creation in a previously unfragmented habitat and the resulting changes in physical abiotic factors. The Response phase includes biotic responses (structural, community composition, species interactions) to edge creation. The final Effect phase denotes potential functional effects of community responses to edge influence and resulting feedback effects on the respondent communities (1.Gehlhausen et al. 2000, 13. Laakso et al. 2000, 3. Laurance et al. 2002, 2. Harper et al. 2005, 7. Vasconcelos and Laurance 2005, 5. Laurance et al. 2006, 4. Piessens et al. 2006, 10. Bolger 2007, 11. Ewers et al. 2007, 9. Ewers and Didham 2008, 6. Malmivaara-Lämsä et al. 2008, 12. Rosenlew and Roslin 2008).

The Afromontane forests of Nigeria are part of the Cameroonian Highlands Ecoregion, an ecologically distinct region that faces considerable conservation threats from intensifying fragmentation and land-use change (Olson et al. 2001b, WWF 2001). This ecoregion comprises a landscape mosaic of unique submontane tropical forest fragments embedded within native montane grasslands that are undergoing rapid land-use conversion to widespread, intensive pastoral grazing and scattered subsistence farming (Hall 1971, Hurault 1998). This is coupled with human-induced fires occurring frequently in the production matrix to stimulate grass re-growth in the dry season, resulting in a highly disturbed and hostile matrix (Chapman et al. 2004). This system provides a unique opportunity to quantify the importance of adjacent matrix restoration in determining the intensity of edge responses in remnant ecosystems due to recent restoration efforts around the Afromontane forest study site. As dung beetles are abundant and widespread, both globally and throughout Afromontane regions (Hanski and Cambefort 1991, Davis et al. 2008), I used this group as a focal taxon to test community responses to these interactive drivers. Additionally, Scarabaeine dung beetle communities in Afromontane regions are responsible for the vast majority of dung removal in these ecosystems (Udy & Nelson, unpub), making the group highly suitable for quantifying the functional consequences of anthropogenic drivers in this severely-fragmented landscape (Kotze and Lawes 2007).

This study will address three main questions that currently require further investigation in the literature. Firstly, in Chapter 2 I quantify dung beetle community responses to human-induced habitat edges and assess the efficacy of adjacent matrix restoration on alleviating these edge effects. In particular, I compare responses in abundance, species richness, and community composition in sites where external anthropogenic threats have been excluded from the adjacent matrix with unprotected degraded sites across continuous edge gradient transects. I also look at variability in responses of dung beetles between species to gain an understanding of how individual species may contribute to community-level responses.

In Chapter 3, I use measurements of morphological traits to explain why species are responding differently to habitat edges and matrix restoration and I test for overall responses in the distribution of functional traits, both within and between species. This is to determine the relative importance of individual species trait variation in community level trait composition, which is likely to be important for explaining variation in ecosystem processes.

Finally, Chapter 4 puts the findings from previous chapters into an ecosystem level context by applying a response-effect trait framework to determine potential cascading effects of environmental change (edge effects and matrix restoration) on dung beetle mediated nutrient cycling rates. This is achieved using hierarchical structural equation modelling to disentangle the relative mediating effects in dung beetle communities on rates of dung removal, such as species trait effects compared to neutral-based mass effects.

The findings generated from these works will be important for advancing current knowledge of how land-use change can alter the ecological integrity of natural systems and importantly, provide insight into the relative benefits of restoring matrix habitat adjacent to these systems. This will become evident through the quantification of community responses across continuous habitat edge gradients, an approach that has never been taken in previous studies of dung beetle responses to anthropogenic land-use change. Furthermore, by comparing trait distributions in communities between degraded and regenerating sites, conclusions from this thesis can be extended to the mechanistic determinants of how communities reassemble during habitat restoration. By using these trait determinants in a framework that also incorporates their relative importance for mediating ecosystem processes, this thesis will ultimately provide new insight into the potential flow-on effects of matrix restoration to ecosystem processes via invertebrate community responses.

Chapter 2: Continuous edge responses reveal off-site effects of matrix restoration in dung beetle communities

2.1 INTRODUCTION

Edge effects are trans-boundary phenomena that result from the abiotic and biotic contrast between two adjoining habitat types (Fonseca and Joner 2007). These effects may represent a modification or intensification of existing processes following the fragmentation of continuous habitat, or may even represent entirely novel and induced phenomena for species in habitat remnants (Murcia 1995, Didham 2010). As edge effects are the result of patch versus matrix contrasts, edge influence on remnant habitat patches cannot be quantified without considering the characteristics of the adjacent matrix habitat. In fact, within-patch dynamics adjacent to edges are likely to be strongly dependent on the context of the surrounding matrix structure (Murphy and Lovett-Doust 2004, Kupfer et al. 2006). As a consequence, two important concepts are required for conducting edge effect studies with predictive and widely applicable conclusions. Firstly, edge studies should be two sided, whereby edge sampling regimes span from within the patch to the adjacent matrix. Despite the fact that edge effects are a product of the flow of materials, energy, and organisms between adjoining habitats, there are still consistently greater numbers of edge effect studies that only take into account one side of the edge gradient (Fonseca and Joner 2007). Secondly, due to the two-sided nature of edge effects, adjacent matrix structure should be taken into account to detect potential interactions between these two drivers of environmental change (Cook et al. 2002, Laurance et al. 2011).

Many studies report important effects of matrix structure on within-patch dynamics and structuring of communities around habitat boundaries. For example, matrix structure has been shown to determine the likelihood and rate of dispersal from habitat patches depending on the 'resistance' (i.e. the level at which dispersal is facilitated, determined by the degree of contrast between matrix and forest) of the surrounding matrix (Ricketts 2001, Haynes and Cronin 2006, Haynes et al. 2007, Laurance et al. 2011). The matrix can also provide habitat for exotic species, which then spill over into adjacent remnant habitats (Cook et al. 2002, Rand et al. 2006). The structure of the surrounding matrix can also have significant impacts on abiotic factors such as microclimatic variables within habitat remnants. For example, Denyer et al. (2006) showed significant changes in photosynthetically active radiation, vapour moisture deficit, and air temperature between habitat edges abutting either a low-contrast pine plantation matrix or a high-contrast pasture matrix. If the physical effects of habitat edges are intensified as demonstrated by Denyer et al. (2006), this is likely to have major impacts on various aspects of the adjacent remnant system as these abiotic factors are important proximate drivers of edge responses in ecological communities (Didham and Lawton 1999, Laurance et al. 2002, Grimbacher et al. 2006, Kappes et al. 2009).

Trans-boundary effects are exacerbated by external anthropogenic processes that impose direct and indirect effects on communities. For example, livestock encroachment into forest remnants and the adjacent matrix can have major impacts on vegetative structure, while increasing soil compaction and nutrient inputs (Smit and Kooijman 2001, Martinez and Zinck 2004, Van Uytvanck and Hoffmann 2009), which can directly alter habitat structure and associated invertebrate communities. Fires are another human-induced disturbance with major impacts on the vegetative structure at habitat edges (Didham and Lawton 1999, Laurance et al. 2011), resulting in intensified edge responses of associated communities. Fires also impose direct negative effects on resident populations, resulting in lowered abundances and species richness in affected areas (Prieto-Benítez and Méndez 2011). These anthropogenic disturbances can also lead to the introduction of further threats such as species invasions (Keeley et al. 2003), resulting in entirely altered matrix habitats which can alter patch-matrix contrast and thus exacerbate edge effects. Through the mediation or exclusion of anthropogenic threats in the adjacent matrix, such efforts may be effective in minimising the detrimental effects of habitat edges (Fonseca and Joner 2007, Laurance et al. 2011).

Multiple threats from habitat loss, edge effects and intensification of land-use practices in the surrounding agricultural matrix combine, frequently synergistically, to exacerbate threats to biodiversity in small habitat remnants (Ewers and Didham 2006a). These interacting drivers of biodiversity loss are especially severe in the rapidly dwindling Afromontane forests of Sub-Saharan Africa, where nature reserves suffer from having the least protection of African conservation areas and high rates of threatened endemic species (WWF 2001, Burgess et al. 2005). The encroachment of anthropogenic threats into natural remnant habitats is ever increasing with Africa's rapidly-growing population. Of particular concern for forest conservation in this region is the rapid increase in the intensification of cattle grazing (Thiollay 2006). As local people in Afromontane regions of Sub-Saharan Africa rely heavily on cattle for their livelihood, increasing human population is closely mirrored by increasing cattle grazing intensity, rapidly leading to the ecological degradation of these regions (Hurault 1998). Furthermore, fires have become more frequent as they are lit to facilitate grass regeneration for pastoralists (Chapman et al. 2004) and impose significant impacts on the landscape in conjunction with intensive cattle grazing (Kotze and Samways 2001). A combination of political instability, poverty, and cultural values that lack appreciation of biodiversity, presents major challenges to conservation. Of the rare conservation efforts that are carried out, these are often unsuccessful throughout this region (Hackel 1999, Oates 1999).

This study investigates the impacts of external anthropogenic disturbances in the surrounding land-use matrix on within-patch dynamics in remnant forest. I quantify these impacts by measuring edge responses of invertebrate communities across forest edges adjacent to heavily-degraded cattle pasture versus forest edges adjacent to protected, regenerating matrix where anthropogenic threats have been removed. To test for these cross-ecosystem impacts of matrix restoration, I used dung beetles (Coleoptera: Scarabaeinae) as a focal taxon. Dung beetles are a highly suitable taxon for quantifying responses to habitat fragmentation as they exhibit high sensitivity to disturbance (Favila and Halffter 1997, Nichols et al. 2007). While dung beetles have been widely studied for their response to anthropogenic land-use change and habitat fragmentation, this study is unique in quantifying continuous responses in dung beetle communities to habitat edges.

Spector and Ayazama (2003) found marked changes in community composition among discrete sampling points at the forest interior, edge, and matrix habitats across a natural forest ecotone. These findings were similar to those of Davis et al. (2000, 2001) and Duraes et al. (2005) who found that dung beetle communities differed greatly across natural ecotone gradients. These studies provide strong evidence for the importance of edge effects in determining changes in community structure of dung beetle fauna. However, this has yet to be tested across habitat edges at a natural-forest/production-matrix interface. There has been a multitude of research that has measured dung beetle community structure at discrete sampling points at edges and associated habitat interior (Estrada et al. 1998, Estrada and Coates-Estrada 2002, Spector and Ayzama 2003, Davis and Philips 2005, Díaz et al. 2010). However, this sampling approach achieves descriptive evaluations of community differences between forest edge and interior habitats without providing a predictive function for spatially explicit edge responses in dung beetle communities. Despite acknowledging the importance of understanding the extent of edge responses by dung beetle communities in fragmentation and land-use-change studies (Escobar et al. 2008), there is still a lack of knowledge of such spatially-explicit responses for dung beetles.

The aim of this study is to investigate the impacts of adjacent matrix degradation resulting from anthropogenic disturbances on the strength and form of continuous edge responses in dung beetle communities. By comparing replicate edge gradients at unprotected edges and sites where anthropogenic threats have been excluded from the adjacent matrix, this study provides insight into the dependence of edge responses of dung beetles on adjacent land-use intensity. By quantifying the influence of adjacent matrix degradation on edge responses, this study aims to identify the relative benefit of implementing buffer zones of matrix restoration adjacent to forest remnants for the conservation of invertebrate communities.

2.2 METHODS

2.2.1 Study Site

The study was conducted at the Ngel Nyaki forest reserve, located on the Mambilla Plateau near the Nigerian/Cameroon border in Taraba State. The forest reserve is an outlying section of a West African forest network within the Cameroon Highlands ecoregion (Olson et al. 2001a, WWF 2001). This region comprises a network of Afromontane forest fragments found at elevations up to 2420 metres with distinct wet and dry seasons and an annual rainfall of approximately 1600 to 2000 mm. The wet season lasts from April to October, during which time the plateau has an average temperature of 26°C ±13°C. The dry season commences in November and lasts until March with temperatures ranging from 16°C - 23°C (Hall 1971, Matthesius et al. 2011).

Ngel Nyaki Forest Reserve was established in 1969 and covers an area of approximately 4600 hectares on the Mambilla plateau. This area comprises a mosaic of overgrazed montane grasslands, degraded streamside forest/shrubland strips, and 720 hectares of dense submontane forest on the escarpment edge (Chapman and Chapman 2001, Chapman et al. 2004, BirdLife International 2011). The forest is of an Afrotropical submontane forest type which has a unique floristic community composition with over 146 vascular plant species, many of which are endemic to Afromontane regions including four IUCN Red Data Listed species. There is obvious stratification into emergent canopy species, sub-canopy, understory, and forest floor species. The emergent canopy is composed of three principal species that can reach heights of up to 46 metres. The crowns of these trees are held well above the sub canopy, which is dense and continuous and ranges from about 10 to 30 metres in height. The forest also harbours many species of lianas and epiphytes, which are highly abundant throughout the understory (Chapman and Chapman 2001). Additionally, there are many species of large mammals including primates such as the endangered chimpanzee *Pan troglodytes ellioti*, the putty nose *Cercopithecus aethiops* and tantalus *Chlorocebus tantalus* monkeys. There are also baboons *Papio anubis,* some colobus monkeys *Colobus guereza* and ungulates including many species of duiker (subfamily: Cephalophinae) (Chapman and Chapman 2001, Chapman et al. 2004, Beck and Chapman 2008)

Between the years 2000 to 2005, Nigeria had the 7th highest net annual loss of forest area in the world, with a loss of approximately 410,000 ha/year (BirdLife International 2011). This is largely due to the rapidly increasing human population densities and severe lack of resources being invested into conservation of Nigeria’s natural remnant ecosystems (Olson et al. 2001a). In the Nigerian highlands, cattle grazing by Fulani pastoralists is the predominant form of agricultural land use. The Fulani people originate from Cameroon and it is thought that they only moved onto the plateau early in the 19th century, rapidly displacing the small subsistence farm-holdings of the local Mambilla people (Hall 1971, Hurault 1998). Therefore, it is only relatively recently that the Mambilla Plateau has been subject to such strong anthropogenic disturbances from intensive and unsustainable cattle grazing.

Despite the conservation status of Ngel Nyaki as a national forest reserve, intensive pastoral activity continues to encroach on the reserve boundaries due to a severe lack of local law enforcement. As the Fulani population increases, the number of cattle follows suit along with an increasing need for more land to be used for pasture. Due to this need for more grazing land, there have been constant attempts by local people to burn into the edges of the forest reserve (Chapman and Chapman 2001, Chapman et al. 2004). The introduction of cattle has facilitated the invasion of *Sporobolus Ludetia* tussock grass, significantly increased soil compaction, and caused major issues with soil erosion resulting in the widespread conversion of native grassland to a low diversity grassland matrix (Chapman et al. 2004). Furthermore, illegal poaching has long posed a threat to many of the plant and animal species within the reserve and has also greatly intensified over recent years. As a result, there has been a major decrease in, and in some cases local extinctions of, mammal populations in Ngel Nyaki Forest Reserve (Chapman and Chapman 2001, Chapman et al. 2004).

An initiative by the Nigerian Montane Forest Project (NMFP) to protect Ngel Nyaki forest reserve from land clearing, burning and cattle grazing by local people was established by fencing off key areas adjacent to the reserve. Fenced exclusion zones were established up to 200 metres outside Ngel Nyaki in the adjacent pasture. Due to social and financial restrictions, these fence lines were only built in a total of four sites (not the entire circumference of the reserve) with the longest fence line spanning just over 1.6 km. In addition to the fence lines, fire breaks were maintained throughout the dry season to prevent the encroachment of human-induced fires from the grazed pasture. Fire breaks were maintained by removing all vegetation down to bare soil within two meters adjacent to the fence. The removal of external anthropogenic threats from the adjacent grassland matrix in multiple locations scattered around the perimeter of the forest reserve presented a unique opportunity to test the influence of these combined threats on dung beetle biodiversity and ecosystem processes.

2.2.2 Study Design

The sampling design was based on a comparison of dung beetle community responses across three replicate forest edge gradients that were fenced to exclude the combined threats of fire and livestock impacts and promote forest regeneration, versus three replicate forest edge gradients that were unfenced and exposed to these combined threats. I refer to these edge gradients as ‘regenerating’ edges versus ‘degraded’ edges, respectively. I selected regenerating sites that had been fenced by NMFP from two to four years prior to this study. The locations of the three regenerating edges and three degraded edges around the perimeter of Ngel Nyaki were interspersed to reduce potential spatial autocorrelation of treatment effects (Figure 2.1). Replicate edge gradients were at least 100 meters apart, therefore edge sites were at least twice the distance apart than was maintained among sampling points within sites.

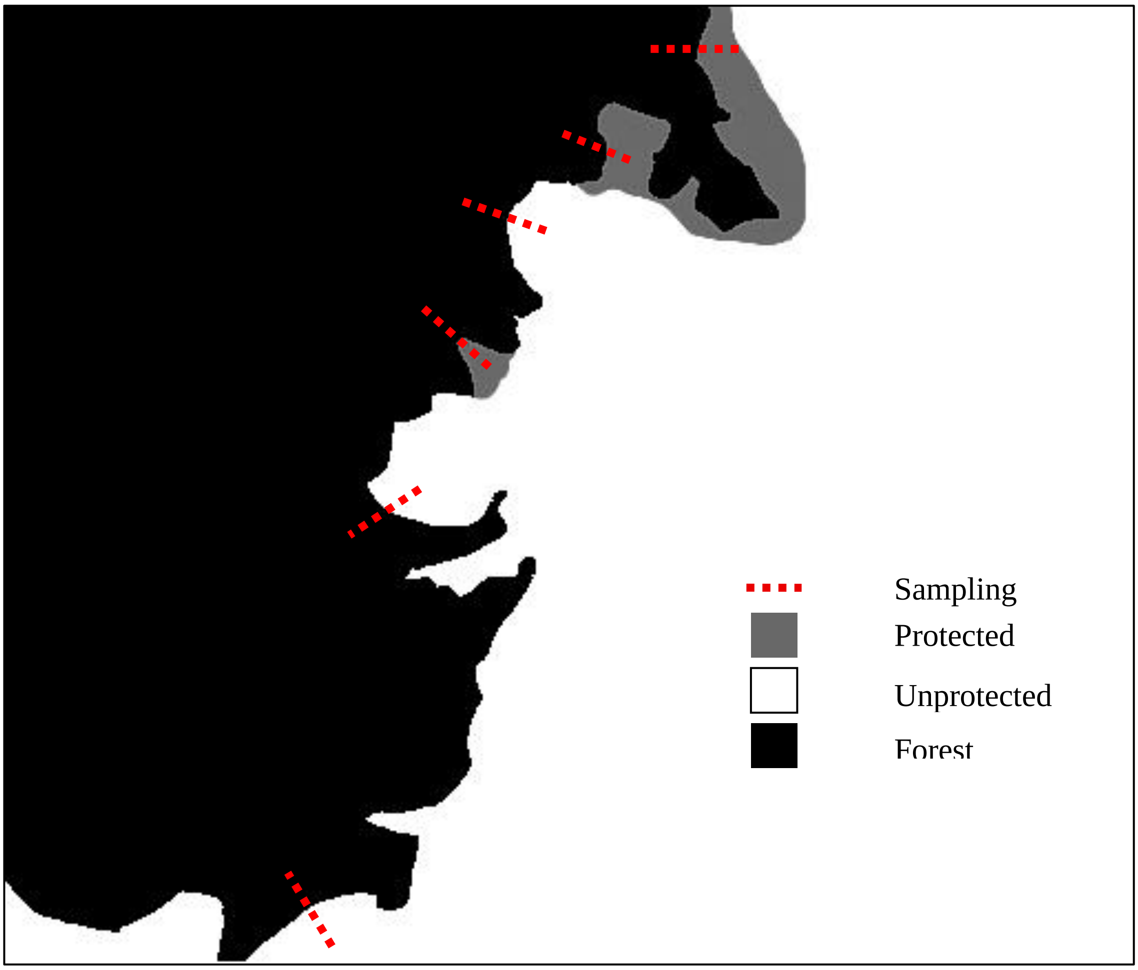


Figure 2.1 Spatial distribution of edge gradient transects at Ngel Nyaki forest reserve.

At each of the three protected and three unprotected edges, sampling points were established at 13 distances along a forest-to-matrix gradient spanning both sides of the forest edge on a doubling scale: -160, -80, -40, -20, -10, -5, 0, 5, 10, 20, 40, 80 and 160 meters, with negative values used to denote forest sites. The edge (0 meters) was defined as the drip line of the outermost canopy trees at the forest edge. This design allowed for the fine-scale detection of rapid ecological responses within close proximity of the forest edge, where edge effects were expected to be most intense, while still allowing for the detection of edge effects over a potentially large spatial extent. Additionally, responses in community structure around the habitat edge are often an asymmetrical product of effects in both the focal habitat and the matrix, therefore sampling was conducted on both sides of the forest edge to account for these trans-boundary processes (Ewers and Didham 2006b, Fonseca and Joner 2007).

The 13 sampling points along each edge gradient were not established in a straight line transect arrangement, as this would have caused potential trap interference and spatial autocorrelation bias (Baker and Barmuta 2006). For example, Larsen & Forsyth (2005) found that in order to maintain trap independence in dung beetle biodiversity studies, the minimum distance between sampling points should be 50 meters, as this just exceeds the distance over which most dung beetles are capable of detecting dung. Therefore, in order to maintain independence between samples, sampling points were staggered laterally, parallel to the forest edge, such that all sampling points were at least 50 meters apart whilst still maintaining their respective distance from the edge (Figure 2.2).

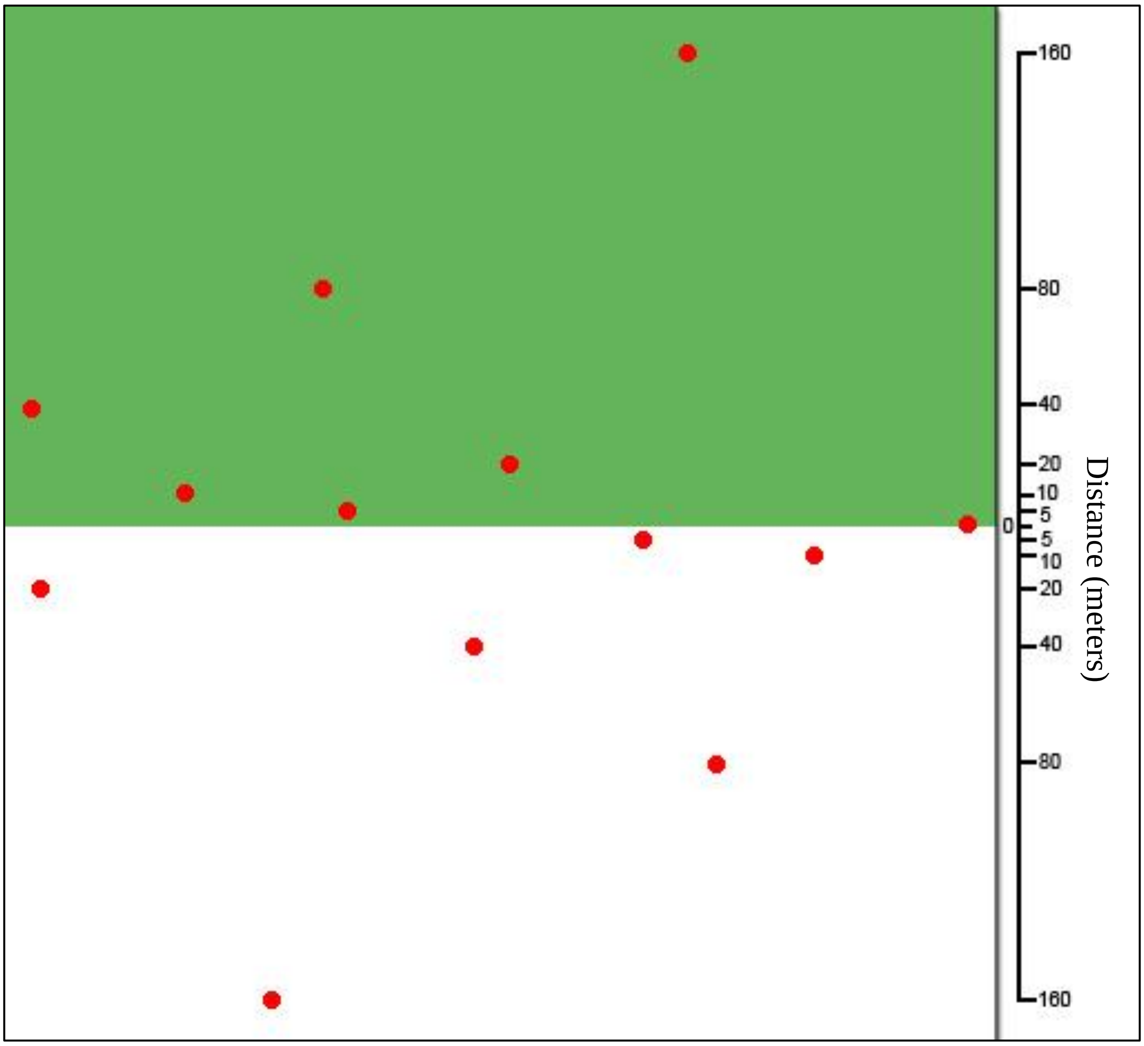


Figure 2.2 Example of a spacing design for one of the edge gradient transects. Red points indicate the location of sampling points with at least 50 meters distance between each point. The green denotes the forest habitat and the opposing white denotes the matrix habitat.

As a further control against potential sampling bias along edge gradients, two ‘dummy’ edge gradients were established as control sites (Baker and Barmuta 2006), with one dummy gradient located in the forest interior at least 640 meters from the nearest grassland edge, and the other located in the grassland matrix interior at least 640 meters from the nearest forest edge. These gradients could then be used to test for trap depletion effects or the effects of geographic distance which may confound the detection of responses across the forest edge gradient (Baker and Barmuta 2006).

2.2.3 Construction of baited pitfall traps

Dung beetles were sampled using dung-baited pitfall traps consisting of 500 ml plastic cups with a depth of 11 cm and diameter of 8 cm, buried so that the rim of the cup was flush with the surface of the ground. To protect the trap from rain and falling debris, a wooden trap cover was held c. 20 cm above the cup using wooden stakes. From this trap cover, dung bait was suspended with string so that the bottom of the bait was level with the rim of the cup. The bait was contained within muslin mesh, which allowed the scent of the bait to easily permeate into the surrounding atmosphere but was fine enough to exclude insects from directly accessing the bait and thus altering its attractiveness. The cup was filled with approximately 200 ml of water and five drops of highly concentrated, odourless, and clear detergent, which served to break the surface tension of the water. Pig dung was used as bait because omnivore dung is recognised as the most widely attractive to dung beetles (Tsbikae et al. 2008). Domestic pigs were reared and fed a consistent controlled diet so that the dung used in the experiments was more likely to be chemically similar and thus similar in attractiveness regardless of the day it was collected.

2.2.4 Sampling dung beetles

Sampling of dung beetle communities was undertaken at the end of the rainy season at Ngel Nyaki Forest Reserve from October 4 to November 29, 2009. One baited pitfall trap was set up for two days at each of the 13 sampling points within each of the six edge gradient sites and two control sites (104 baited pitfall trap locations in total). For logistical reasons only one edge gradient could be sampled at a time, so the temporal sequence in which sites were sampled was randomised. At any given site, all 13 traps were set on the same day, no later than 3 pm, and the order in which the traps were baited was also fully randomised. Each trap was baited with 40 g fresh pig dung (no older than 12 hours) and left for approximately 24 hours. Samples were then collected and the traps reset with fresh bait for a further 24 hours. The second day’s dung beetle collection was then pooled with the first days to obtain a single 48-hour sample per trap for analysis. Variation in abundance per trap is dependent on both beetle density in the vicinity of the trap and relative activity rates in response to the dung bait and environmental conditions. I refer to the number of individuals per trap as a measure of dung beetle ‘capture rate’. To ensure there was no bias in dung attractiveness between traps across the edge gradient, all the dung used for an entire site came from a single homogeneous batch. Each batch consisted of dung collected periodically throughout the previous 12 hours to ensure freshness and maximum attractiveness, and thoroughly mixed to ensure consistent moisture and chemical content across baits.

2.2.5 Sorting and identifying dung beetles

All dung beetles in the subfamily Scarabaeinae were removed from the baited pitfall samples and preserved in 70% alcohol. Specimens were sorted to genus and assigned to initial ‘morphospecies’ groupings based on consistent morphological traits such as exoskeletal colouration, body size, and external structures. Formal species identification was then undertaken by Rowan Emberson at the Lincoln University entomology collection and Frank Krell at the Denver Natural History Museum. Taxonomic knowledge of the Nigerian montane dung beetle fauna is comparatively limited and not all morphospecies could be assigned to known species.

2.2.6 Statistical analysis

2.2.6.1 *Calculating sampling effort and standardised richness*

The completeness of sampling was assessed using sample-based species accumulation curves in EstimateS 8.2 (Colwell 2009). Mau Tao estimated species richness and the frequency of singletons (species represented by only one individual randomly drawn from a given sample) were calculated from 100 replicate random draws (without replacement), and accumulation curves were rescaled to the number of individuals captured.

Species richness per sample often varies as an artefact of sample abundance (Colwell 2009), so in order to standardise for potentially spurious sampling effects I conducted a species rarefaction analysis using BDPro v3.2 (McAleece 1997). Rarefaction involved an individual-based randomisation procedure in which the number of species at each site was estimated after first standardising to the highest sample abundance common across sites. I chose a conservative rarefaction cut-off (knot) of n=21, with sites having total sample abundance smaller than this cut-off being dropped from the analysis. Samples that were excluded were 12 (out of a total of 36) samples from regenerating edge sites and 21 (out of 37) from degraded edge sites. A lower cut-off value would have included more sites, but would have rapidly weakened the value of the comparison, as the low abundance of the random draw constrains the range of possible variation in species richness.

2.2.6.2 *Measuring responses in community composition*

To analyse differences in species composition, I calculated base 10 Modified-Gower dissimilarity values among all samples (Anderson et al. 2006, Anderson et al. 2011) using the PRIMER v6 software package (Clarke and Gorley 2006). The Modified-Gower distance metric considers an order-of-magnitude change in abundance (e.g., from 0.01 to 0.1) equal to a change in composition (i.e. from 0 to 1 species), which therefore accounts for the changes in relative abundance of species in addition to changes in the community composition *per se*. This approach allowed for the explicit specification of the importance given to changes in species relative abundance vs. changes in composition in the analysis (Anderson *et al.* 2006).

In order to attain a preliminary indication of how species composition responds to varying matrix degradation, distance from edge, or their interaction, I used the Modified-Gower resemblance matrix to perform a permutational distance multivariate ANOVA in the PERMANOVA package in PRIMER V6 (Anderson et al. 2008). ‘Distance from the forest edge’ and ‘matrix degradation’ were both treated as fixed effects, including the interaction term between the two predictors. ‘Site’ (representative of each replicate edge gradient) was specified as a random factor in order to allocate the correct error term for the model. The PERMANOVA analysis served as a first step in understanding community responses but was unable to describe the functional form of continuous edge responses under varying adjacent matrix degradation. I used non-metric multidimensional scaling (NMDS) to visually compare community composition between samples across degraded and regenerating forest-to-matrix edge gradients, including the forest and pasture reference sites as points of reference. The individual and cumulative contribution of species to overall compositional dissimilarity was calculated using the SIMPER function in PRIMER. From this analysis, I then selected the species with the highest contributions to compositional changes that had sufficient numbers and spatial distributions to test continuous edge response functions in individual capture rates.

2.2.6.3 *Quantifying edge response functions for dung beetle communities*

Continuous edge response functions were calculated for total dung beetle capture rate, species richness, rarefied species richness, community similarity, and capture rates of each of the sufficiently abundant species that explained the most variation in community similarity determined by the SIMPER test. To test edge response functions for community composition, I calculated the average similarity of each sample to the forest reference site using the Modified-Gower resemblance matrix. This calculation provides a vector that indicates compositional dissimilarity of sampled communities from the forest reference communities, which can then be used as a response variable in univariate statistical analyses. These functions were analyzed across patch-to-matrix gradients for each of the two levels of habitat edge protection, using the statistical approach of Ewers & Didham (2006b). Using a form of the general logistic model I determined the best-fit edge model out of five models of increasing complexity (Ewers and Didham 2006):

(1) the null hypothesis of no discernable edge effect, calculated as the mean of the response variable η:

$$\eta = \overline{\eta} + \varepsilon$$

where ε is an error term;

(2) a simple linear gradient of the form:

$$\eta_D = \beta_0 + \beta_1 D + \varepsilon$$

where β_0 and β_1 are constants and *D* is the distance to edge;

(3) a power model:

$$\eta_D = \beta_0 + \beta_1 e^{\beta_2 D} + \varepsilon$$

(4) a logistic model that describes a sigmoidal change in community composition across an edge, with an asymptote in both the patch and matrix habitats:

$$\eta_D = \beta_0 + \frac{\beta_1 - \beta_0}{1 + e^{(\beta_2 - D)\beta_3}} + \varepsilon$$

which also includes an additional constant, β_3;

(5) a unimodal model based on the logistic model, but with one extra constant (β_4) and a D^2 term to describe a unimodal change in community composition at a particular distance from an edge:

$$\eta_D = \beta_0 + \frac{\beta_1 - \beta_0}{1 + e^{(\beta_2 - D + \beta_4 D^2)\beta_3}} + \varepsilon$$

I fitted these five models to forest-to-matrix edge gradients, treating the three edge gradients within each of the two matrix restoration treatments (degraded versus regenerating matrix) as replicates. In each case, I assessed model significance and calculated the Akaike Information Criterion (AIC) value for each model. I selected the best model as the one with the lowest AIC value, or in the case of multiple models within two AIC units of each other, I selected the simplest model (with the fewest parameters). Model fitting was conducted in R version 2.5.1 (R Development Core Team 2004).

2.3 RESULTS

A total of 4705 dung beetles comprising 35 species in 11 genera were captured across all sites (Table 2.1). Overall, the community was dominated by the genus *Onthophagus* with 19 species which accounted for 54% of total beetle abundance, followed by the next most speciose genera *Catharsius* and *Proagoderus*, each with only three species (Table 2.1). Species accumulation curves revealed that sampling effort was adequate to characterize the local dung beetle community likely to be attracted to omnivore dung across different surrounding land-use treatments, with estimated species richness near an asymptote and the number of singleton species starting to decline with increasing sampling effort (Figure 2.3). Over 40% of species collected were matrix specialists which occurred exclusively in pasture samples, while 28% of species were captured exclusively in forest samples. The remaining 30% of the species collected were found to occur across both habitats (Table 2.1).

Table 2.1 List of morphospecies and their occurrence across habitat (forest and pasture) and adjacent matrix type (R = regenerating, D = degraded) with the total number of individuals per species.

Species	**Habitat**	**Adjacent Matrix**	**Individuals**
Caccobius sp.1	Pasture	R, D	4
Caccobius sp.2	Pasture	R	1
Catharsius dux	Pasture	R, D	12
Catharsius sp.2	Forest	R, D	7
Catharsius sp.3	Pasture	D	1
Diastellopalpus nigerimus	Forest	R, D	65
Diastellopalpus tridens	Forest	R	3
Latidrepanus caelatus	Forest, pasture	R, D	40
Heliocopris myrmidon	Pasture	R, D	3
Liatongus arrowi	Forest	R	1
Neosisyphus armatus	Forest, Pasture	R, D	6
Onitis sp.1	Pasture	D	10
Onitis sp.2	Pasture	D	1
Onthophagus sp.1	Forest	R, D	198
Onthophagus sp.2	Forest, pasture	R, D	2131
Onthophagus sp.3	Forest, pasture	R, D	1787
Onthophagus sp.4	Forest	R, D	4
Onthophagus sp.5	Forest, pasture	R, D	27
Onthophagus sp.6	Forest, pasture	R, D	164
Onthophagus sp.7	Forest	R, D	24
Onthophagus sp.8	Forest	R, D	35
Onthophagus juvencus	Pasture	R, D	7
Onthophagus alternans	Forest, pasture	R, D	41
Onthophagus sp.11	Forest	D	2
Onthophagus rufonotatus	Pasture	R, D	14
Onthophagus sp.13	Forest, pasture	R	31
Onthophagus sp.14	Pasture	R, D	7
Onthophagus sp.15	Forest	R, D	7
Onthophagus longipilis	Pasture	R, D	9
Onthophagus sp.18	Pasture	R	1
Onthophagus sp.19	Pasture	R	2
Onthophagus sp.21	Pasture	D	1
Proagoderus elgoni	Pasture	R, D	14
Proagoderus multicornis	Forest	R, D	9
Sisyphus sp.1	Pasture	R	31

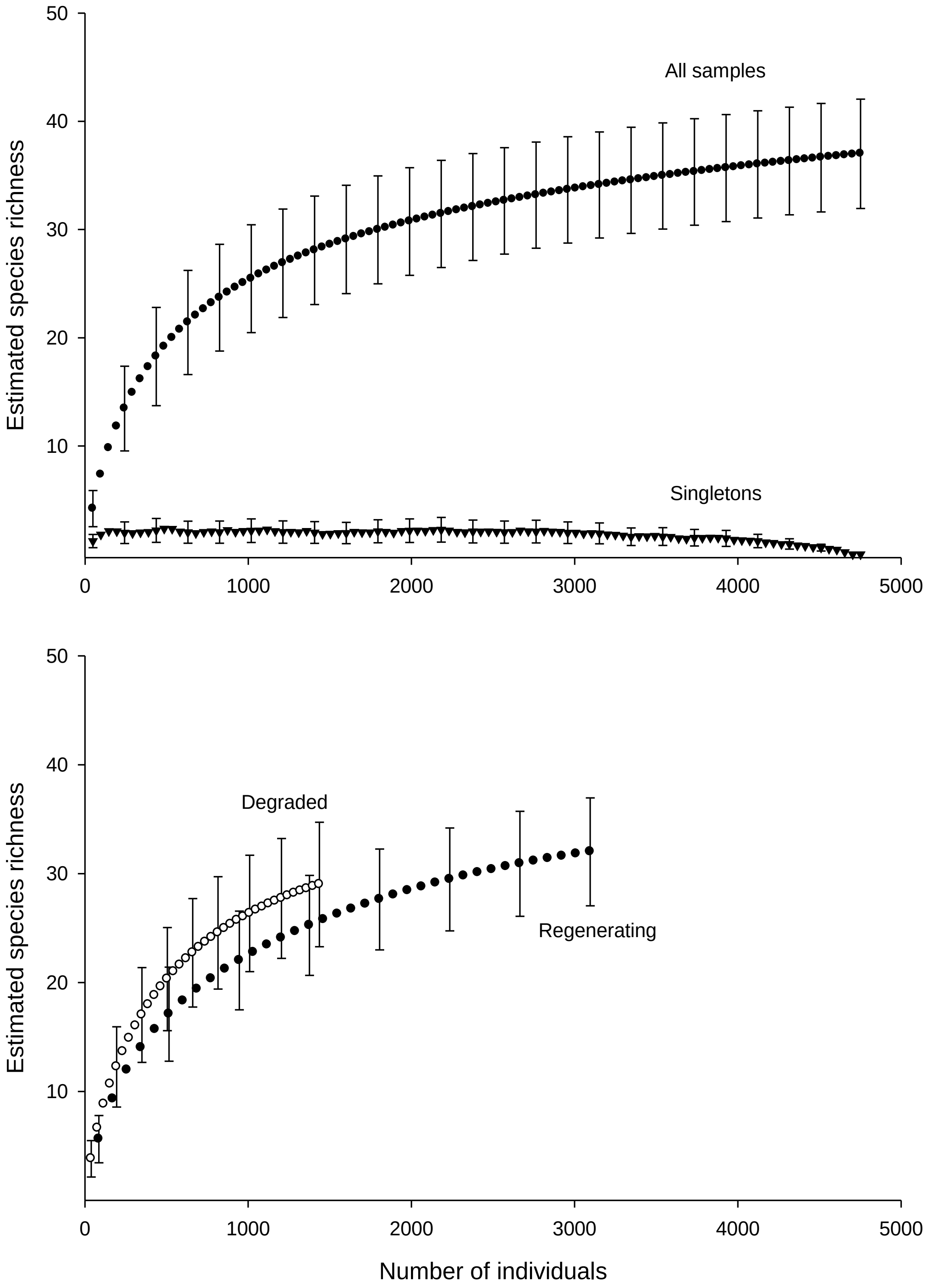


Figure 2.3 Sample-based species accumulation curves, re-scaled to number of individuals per sample, for (a) all 104 baited pitfall trap samples, and (b) regenerating vs. degraded edge gradients. Values are mean (± 95 % confidence intervals) estimated species richness from 50 random draws at any given number of samples. Singletons are species that were represented by only one individual across all samples.

2.3.1 Regeneration of adjacent matrix restores high dung beetle abundances

Total abundances of dung beetles were found to change significantly across the forest-to-matrix edge gradient (Figure 2.4), with strong logistic response functions evident for both the degraded and regenerating edge gradients (Table 2.2). For both levels of matrix degradation, highest abundances were found in the forest habitat, and lowest abundances in the matrix habitat, with a zone of rapid change found just outside the forest edge. More importantly however, I found a 43% increase in the magnitude of edge effects at regenerating edges compared to degraded edges, driven by a 20% increase in average beetle abundance within regenerating matrix sites, and a 53% average increase in dung beetle abundance in forest sites adjacent to a regenerating matrix (Figure 2.4).

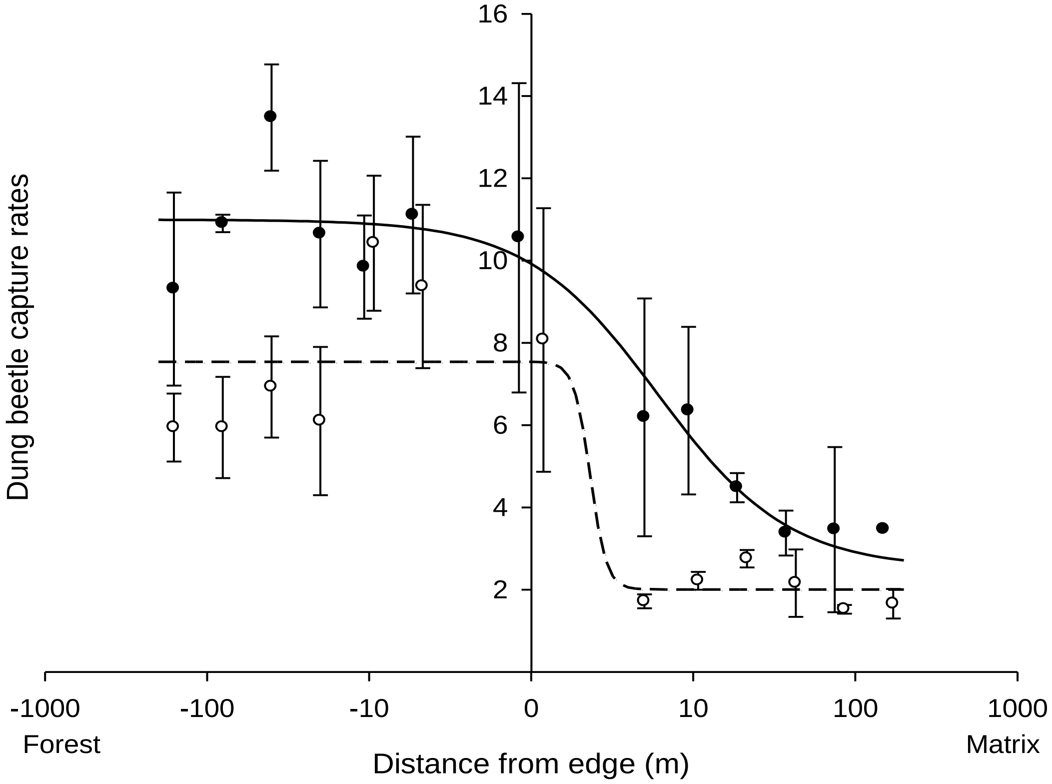


Figure 2.4 Square root-transformed capture rates of dung beetles in baited pitfall traps (mean ± 1 SE) across regenerating (closed symbols and solid fitted line) and degraded (open symbols and dashed fitted line) edge gradients. Negative values on the x-axis indicate forest sites. Lines are the best-fit continuous edge response functions of five fitted models of increasing complexity. Overlapping data points are offset for clarity.

Table 2.2 AIC scores obtained from the edge function fitting procedure for models of increasing complexity (null, linear, exponential, logistic, and unimodal) for both regenerating and degraded edge gradients. Species in the response column refer to capture rates of each species. Bold AIC scores indicate the model of best fit.

Response	Null	Linear	Exponential	Logistic	Unimodal
Regenerating Matrix					
Abundance	229.629	203.526	NA	**201.38**	256.617
Richness	**160.874**	162.778	164.779	NA	NA
Rarefied richness	**67.37**	69.318	NA	NA	NA
Community similarity	-30.83	**-33.296**	-31.294	-31.494	NA
Onthophagus sp.1	123.035	**101.17**	NA	103.376	109.559
Onthophagus sp.2	219.383	166.712	NA	**164.855**	NA
Onthophagus sp.3	217.13	211.788	NA	**204.635**	NA
Onthophagus sp.5	17.084	11.616	NA	NA	**4.768**
Onthophagus sp.6	-25.35	-25.915	NA	NA	**-33.184**
Onthophagus sp. 7	33.024	23.96	NA	**20.018**	16.994
Onthophagus sp. 8	-12.172	-20.904	NA	NA	**-23.644**
Onthophagus alternans	**-39.532**	-39.162	-37.203	NA	-37.344
Onthophagus sp.13	42.252	42.211	NA	NA	**31.813**
Diastellopalpus nigerimus	74.454	51.522	NA	**46.848**	46.685
Latidrepanus caelatus	68.019	67.58	NA	NA	**58.272**
Proagoderus elgoni	-7.257	**-8.339**	-6.338	NA	NA
Sisyphus sp.1	71.071	67.021	68.679	68.306	**66.086**
Degraded Matrix					
Abundance	214.74	197.365	NA	**186.412**	243.325
Richness	170.029	**162.2**	NA	165.902	NA
Rarefied richness	**59.017**	59.942	NA	61.939	59.498
Community similarity	-11.596	-21.434	NA	**-32.488**	NA
Onthophagus sp.1	74.616	**67.801**	NA	NA	68.937
Onthophagus sp.2	195.153	173.598	NA	**173.023**	NA
Onthophagus sp.3	196.297	191.927	NA	NA	**168.095**
Onthophagus sp.5	-25.35	-25.915	NA	NA	**-33.184**
Onthophagus sp.6	-4.864	-2.93	NA	NA	NA
Onthophagus sp.7	-25.35	-26.605	NA	NA	**-33.695**
Onthophagus sp.8	6.154	0.354	NA	NA	**-3.011**
Onthophagus alternans	**1.415**	1.427	NA	NA	3.404
Onthophagus sp.13	**-71.969**	-70.057	NA	NA	NA
Diastellopalpus nigerimus	7.112	**-0.192**	1.808	2.843	NA
Latidrepanus caelatus	**-47.104**	-46.042	NA	NA	NA
Proagoderus sp.1	-33.585	**-38**	NA	NA	-37.948
Sisyphus sp.1	35.162	**30.748**	NA	NA	30.935

2.3.2 Weak positive effect of matrix degradation on dung beetle species richness

The edge function fitting procedure revealed a null response in species richness across the edge gradient in regenerating sites. In contrast, I found a significant linear response across degraded edges whereby species richness decreased with increasing distance into the matrix habitat (Figure 2.5, Table 2.2). However, after calculating rarefied richness at standardized sample abundance, I found that edge responses in species richness were driven entirely by variation in dung beetle abundance with null responses across both edge types (Figure 2.5, Table 2.2).

2.3.3 Differential responses of community composition to habitat degradation

The multivariate PERMANOVA demonstrated that differences in community composition were predicted by distance from the forest edge (Pseudo-F = 4.573, P = 0.001) and also by the exclusion of anthropogenic threats from the adjacent matrix (Pseudo-F = 5.644, P = 0.001). Additionally, there was a significant interaction between these two drivers of compositional changes (Pseudo-F = 1.264, P = 0.023). These differences in community composition were demonstrated in the NMDS ordination whereby the largest differences visible are between matrix and forest communities (Figure 2.6). Surprisingly, the degraded forest communities were more similar to those of the forest reference site than the regenerating forest samples. Similarly, the degraded pasture samples more closely resembled the pasture reference samples in ordination space. The SIMPER analysis revealed that 19 species explained >90% of variation between degraded versus regenerating edge gradient sites. Included within this group that explained the majority of variation were the 13 most abundant species that had ≥13 individuals per site, cumulatively contributing to 81% of variation between matrix degradation treatments (Table 2.3).

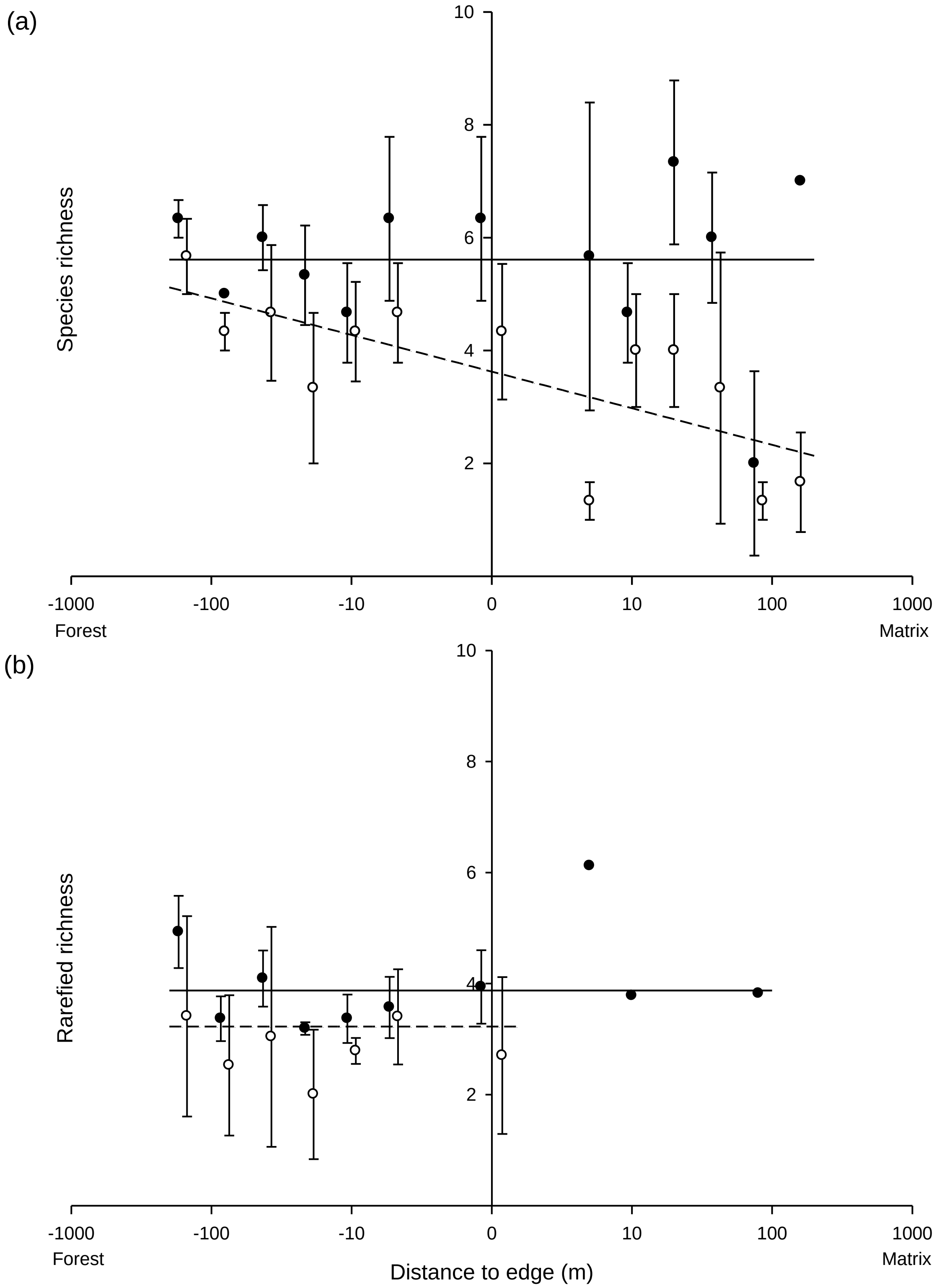


Figure 2.5 Unstandardised species richness (a) and rarefied richness with standardised sample abundance of n ≥ 21 (b) (mean ± 1 SE) across degraded and regenerating edge gradients. Symbols and lines as in figure 2.4. Missing values in (b) are due to sample abundances of < 21 being dropped from the rarefaction analyses. Overlapping points are offset for clarity.

Table 2.3 Output from the SIMPER analysis in PRIMER V6 indicating the amount of community dissimilarity explained by individual species between degraded and regenerating edge gradient sites. Mean dissimilarity is from a Bray-Curtis resemblance matrix with standard deviation and the percent contribution of each species to the overall site dissimilarity. † denotes species with ≥13 individuals.

Species	Mean dissimilarity	Dissimilarity SD	Contribution %	Cumulative contribution %
Onthophagus sp. 1†	9.41	1.01	16.20	16.20
Onthophagus sp. 6†	8.63	0.59	14.86	31.06
Onthophagus sp. 3†	8.35	0.90	14.37	45.43
Onthophagus sp. 1†	3.01	0.80	5.18	50.62
Latidrepanus caelatus†	2.84	0.59	4.89	55.50
Diastellopalpus nigerimus†	2.39	0.81	4.11	59.61
Sisyphus sp. 1†	2.38	0.35	4.09	63.71
Onthophagus sp. 5†	2.33	0.52	4.01	67.72
Onthophagus sp. 13†	2.30	0.62	3.96	71.67
Onthophagus alternans†	1.72	0.48	2.96	74.63
Onthophagus sp. 7†	1.68	0.71	2.89	77.52
Onthophagus sp. 16	1.21	0.43	2.08	79.61
Proagoderus elgoni†	1.21	0.39	2.08	81.69
Onthophagus sp. 8†	0.95	0.56	1.63	83.32
Onthophagus sp. 14	0.85	0.35	1.47	84.79
Onitis sp. 1	0.83	0.27	1.43	86.22
Proagoderus multicornis	0.82	0.55	1.41	87.63
Onthophagus juvencus	0.75	0.36	1.28	88.92
Catharsius dux	0.73	0.28	1.26	90.17

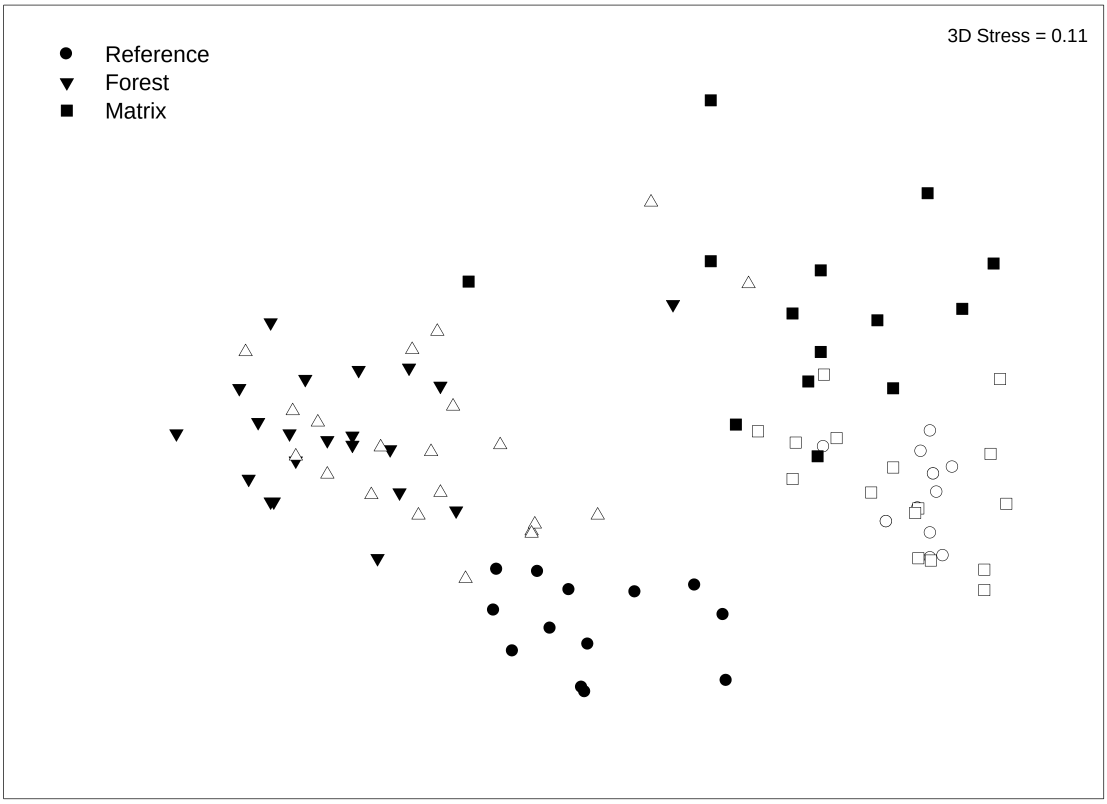


Figure 2.6 Non-metric multidimensional scaling ordination plot comparing dung beetle species composition between protected and unprotected forest edges, using a modified-Gower dissimilarity metric. Each point represents a baited pitfall trap sample taken from a given distance from the edge. Open symbols represent degraded sites and closed symbols represent regenerating sites. Forest and pasture reference sites are located at least 640 meters from the forest edge

The shape of edge response functions in dung beetle community composition varied significantly with matrix restoration (Figure 2.7, Table 2.2). As might be expected, dissimilarity increased across forest-to-matrix edge gradients. However, matrix restoration did not appear to lead to a significant decrease in dissimilarity values for either matrix or forest assemblages. Instead, communities at regenerating edge gradients were found to gradually converge in compositional similarity with reference communities, similar to that seen in the degraded sites, which showed a rapid turning point in compositional change at 20m into the forest. Therefore, these sites actually showed greater similarity to the forest reference than the regenerating edge gradient communities further into the forest.

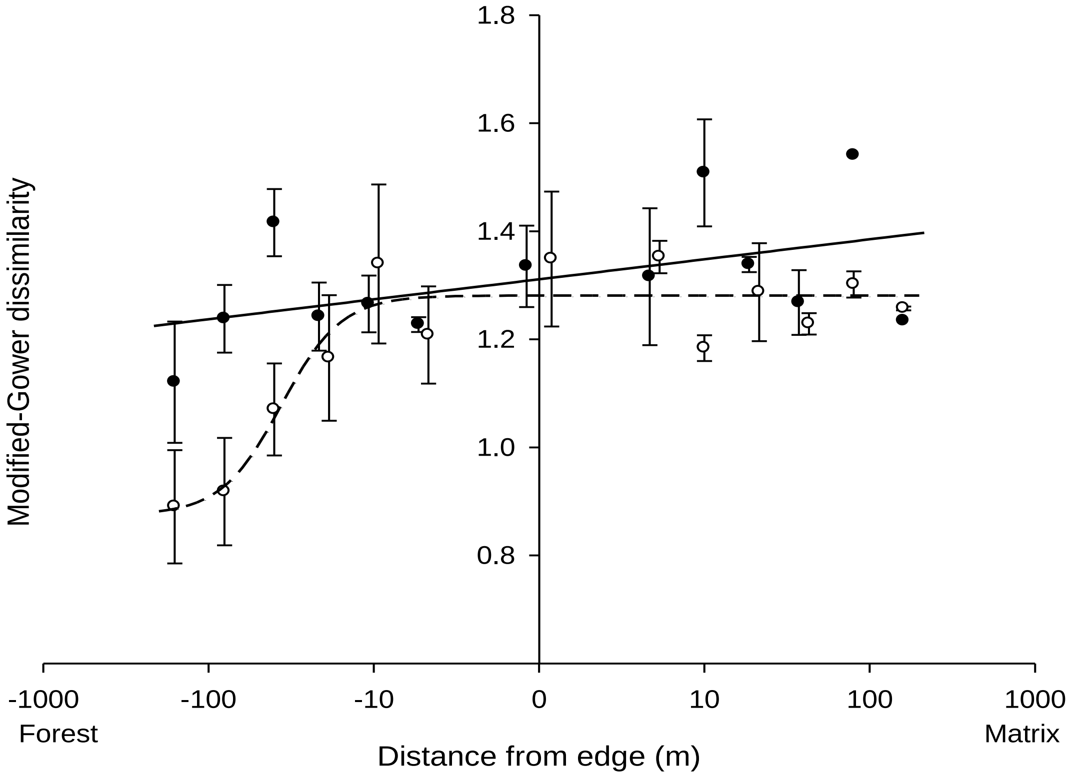
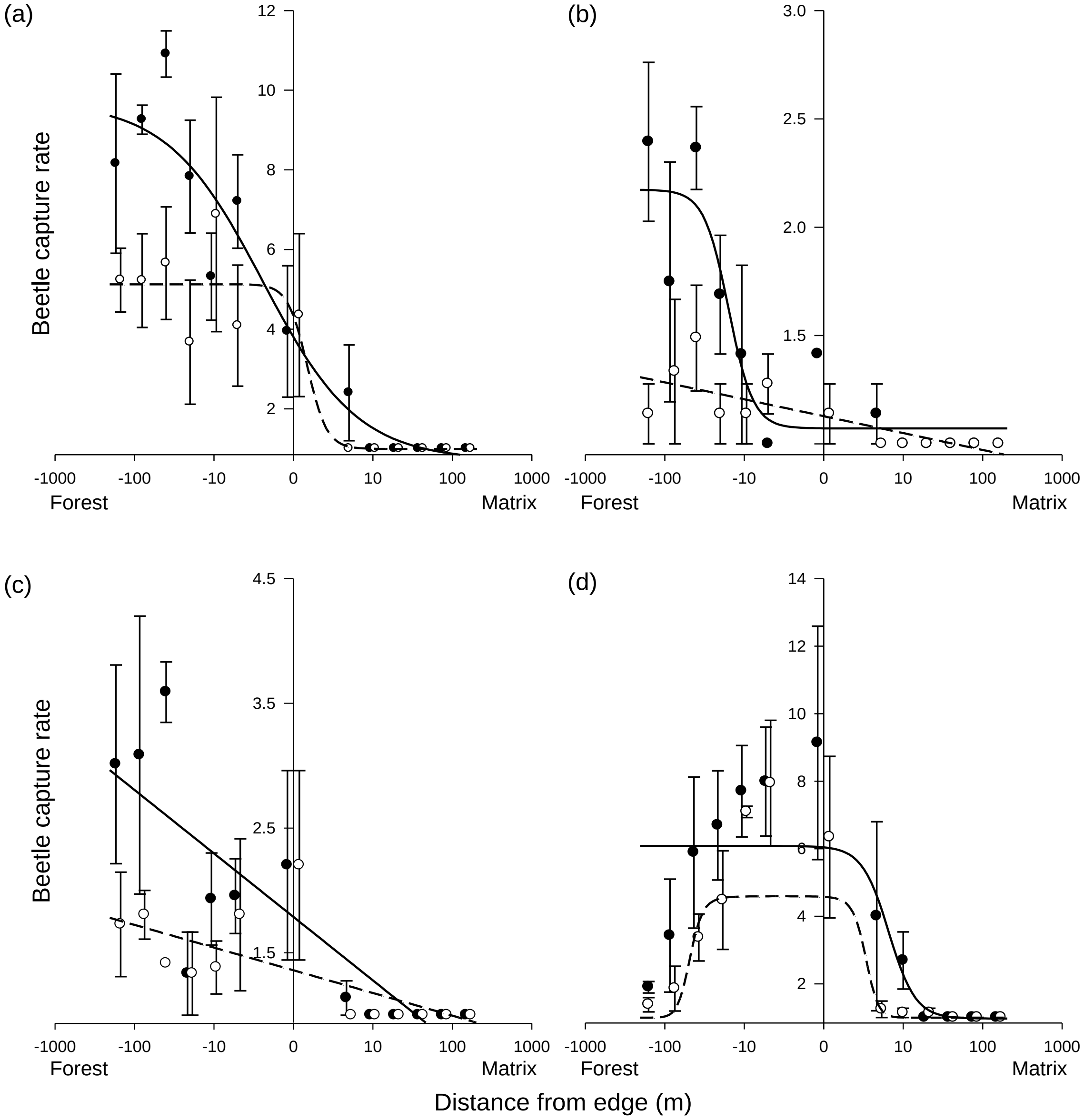


Figure 2.7 Dissimilarity of community composition (mean ± 1 SE) at edge gradient sampling points to forest interior communities across degraded versus regenerating edge gradients. Negative values on the x-axis indicate forest sites. Symbols and lines as in Figure 2. Overlapping data points are offset for clarity.

2.3.4 Adjacent matrix degradation alters within-species response magnitude

Overall, 65% of the 35 species collected had higher total capture rates in regenerating compared to degraded edge gradient sites. Out of the total 35 species, 13 had sufficient numbers of individuals and distributions across samples to test species responses to edge effects along degraded and regenerating edge gradients, 11 of which had higher total capture rates across regenerating sites. Fully 12 out of the 13 species tested responded significantly to edges (Table 2.2) and 10 of these species had significantly different response magnitudes between the degraded and regenerating edge gradients. For example, *Onthophagus* sp.2 displayed sigmoidal responses across both regenerating and degraded edges, with capture rates declining dramatically from forest to matrix habitat, but there was a 79% decrease in edge magnitude in the degraded edge response function when compared to that of the regenerating edge response function (Figure 2.8). In contrast, 8 out of the 13 species tested for continuous responses fit different response functions depending on edge protection. For example, *Diastellopalpus nigerrimus* displayed a sigmoidal response in relative capture rate across regenerating edges compared to a linear response at degraded edges (Figure 2.8).



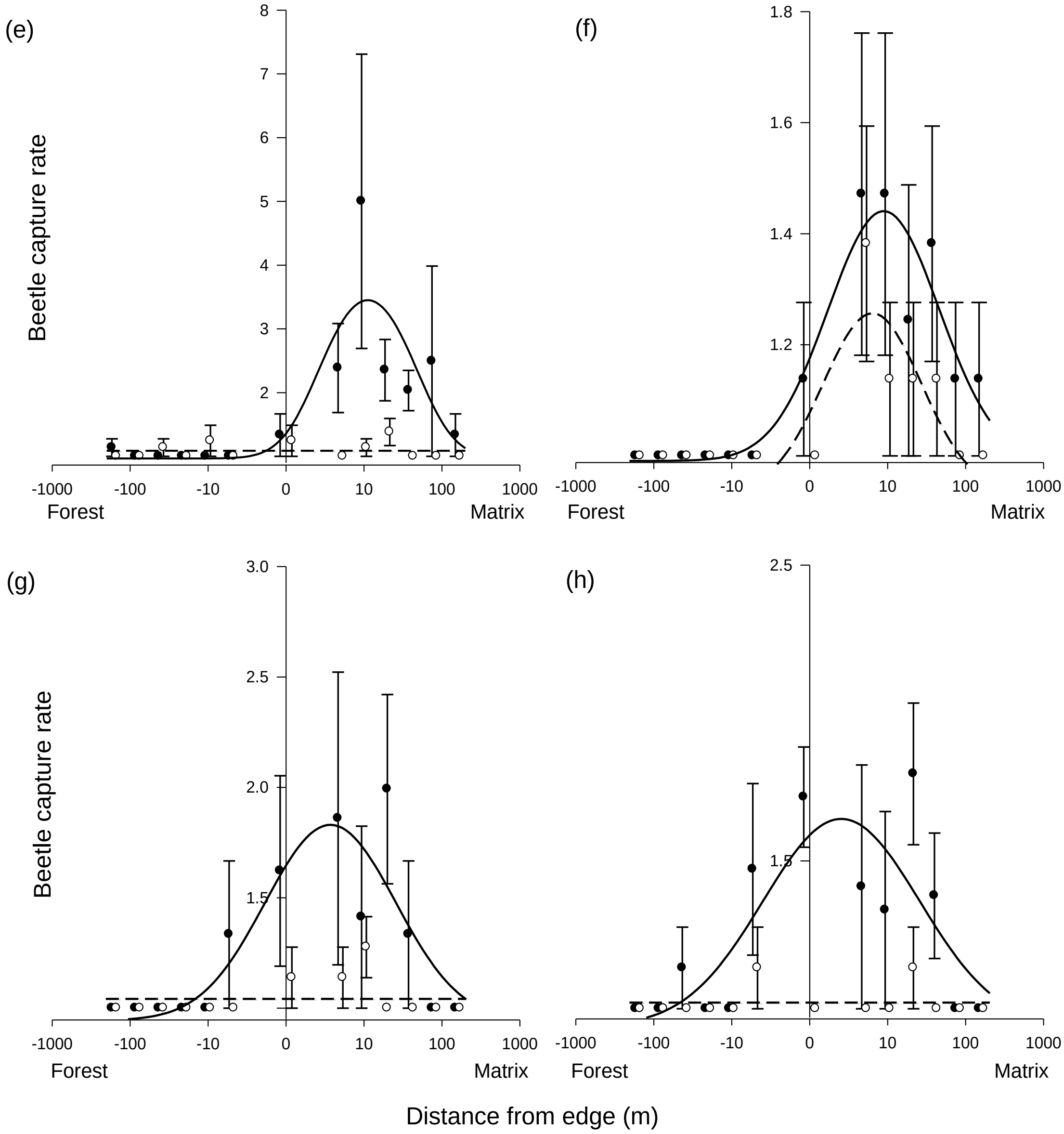


Figure 2.8 Square root-transformed capture rate of dung beetles (mean ± 1 SE) for the eight species of dung beetles that explained the most variation in community compositional changes between regenerating and degraded edge gradients. Species are (a) *Onthophagus* sp.2, (b) *Diastellopalpus nigerimus*, (c) *Onthophagus* sp.1, (d) *Onthophagus* sp.3, (e) Onthophagus sp.6, (f) *Onthophagus* sp.5, (g) *Latidrepanus caelatus* and (h) *Onthophagus* sp.13. Symbols and lines as in figure 2.4. Overlapping data points are offset for clarity.

2.4 DISCUSSION

In highly degraded and fragmented landscapes, edge effects are a dominant driver of biodiversity loss in natural forest remnants (Ewers et al. 2007, Banks-Leite et al. 2010) and without measures to mitigate such effects, remnant populations face gradual decline toward extinction (Laurance et al. 2011). In remnant Afromontane forests in Nigeria, I found dramatic evidence of the negative impacts of human encroachment, livestock overgrazing and uncontrolled burning in the adjacent matrix on dung beetle community responses at remnant forest edges. Over 90% of species responded strongly to edge effects, with up to an order of magnitude decline in dung beetle abundance from the forest to matrix habitats. These results support previous findings that dung beetle communities are highly sensitive to anthropogenic disturbances (Nichols et al. 2007) and provide sobering evidence that external anthropogenic threats can have strong impacts on within-patch community dynamics. Attempts to mitigate these threats through the exclusion of cattle grazing and fires at the Ngel Nyaki forest reserve were shown to have equally dramatic positive effects on dung beetle communities. Less than three years after fencing off relatively small areas of matrix habitat to remove threatening processes, dung beetle communities in adjacent forest edges showed an overall 53% increase in total abundances within these restoration zones. Furthermore, this restoration effort has even led to the re-establishment of certain matrix specialist species that were otherwise absent in the unprotected degraded matrix. These findings suggest that through the mitigation of external anthropogenic threats adjacent to nature reserves, dung beetle communities are likely to respond strongly to such efforts.

2.4.1 Cross-ecosystem impacts are driven by adjacent matrix condition

Species composition underwent rapid turnover at the habitat edge regardless of matrix type. However, changes in community composition across edges differed markedly between the degraded and regenerating edge gradients. This is likely to be explained by differences in vegetative structure and anthropogenic disturbances across the two types of adjacent matrix. The degraded matrix had very low vegetative biomass, diversity, and stratification compared to the regenerating matrix (Campbell 2010). As a result, only certain species of dung beetles would be capable of persisting in the resulting higher temperatures and lower moisture levels of the degraded pasture. The absence of vegetative stratification would also prevent the local persistence of dung beetle species that use a “perch-and-wait” foraging strategy (Hanski and Cambefort 1991, Howden et al. 1991). Furthermore, disturbance frequency (i.e. grass fires and cattle trampling) would limit degraded pasture communities to species that are highly mobile and can re-colonize these areas quickly. Resource availability is also likely to differ largely between the two matrix types due to the exclusion of cattle grazing and thus cattle dung deposited in the regenerating areas. Therefore, it is likely that species with large resource requirements would be unable to survive in the regenerating grasslands. Additionally, the unprotected pasture matrix is constantly subjected to trampling by grazing cattle which has been shown to significantly increase soil compaction (Martinez and Zinck 2004). This can have significantly detrimental impacts on dung beetle communities as only particular species can deal with higher levels of soil compactness when excavating nests (Navarrete and Halffter 2008).

Perhaps the most striking result of this study is the disparity in capture rates and species composition of forest samples taken between regenerating and degraded edge gradients. With a 53% overall decrease in dung beetle capture rates in degraded forest samples, these findings suggest that anthropogenic disturbances occurring in the matrix are imposing offsite impacts on these forest communities. The increased abruptness and openness of the patch-matrix interface (Campbell 2010) is likely to be responsible for such offsite effects that would increase the severity of abiotic edge effect parameters such as wind disturbance, temperature stochasticity, and aridity (Didham and Lawton 1999, Laurance et al. 2002). However, this leads to the question of why there is such a difference in community composition (i.e. relative abundances of species) as opposed to equal changes in abundance across species? In order to better understand such disparity between these species assemblages, it is necessary to disentangle the variable species responses within the community.

2.4.2 Seven out of ten species are affected by adjacent matrix degradation

Almost all continuous response functions tested for individual species were found to differ considerably between protected and unprotected edge gradients. These differences in species responses underscore the surprising differences in community wide response functions between the two types of edge gradients used in this study. This is demonstrated by the 13 species that explained >81% of overall community dissimilarity between levels of edge protection, where 10 of these 13 species displayed striking differences in edge responses between protected and unprotected habitat edges.

For example, *Onthophagus* sp.2, *Onthophagus* sp.1, and *Diastellopalpus nigerrimus* all responded with a higher magnitude of edge response in the regenerating edge gradients due to much higher abundances within the regenerating forest zones.

These differences in response functions could be explained by these species' variable tolerances or habitat preferences. For example, particular microhabitat requirements vary between species such as the need for a dense understory for perch-and-wait foraging strategies often used by smaller dung beetles (Hanski and Cambefort 1991). Another possibility is that because desiccation resistance for invertebrates can be highly variable across species due to various morphological characteristics, differences between these protected and unprotected forest edges in temperature and humidity may place physiological constraints on particular species with lower resistance (Chown et al. 2002). The microclimatic conditions within the degraded habitats are likely to be more severe (Denyer et al. 2006) and therefore these physiological constraints lower the survival of specific sensitive species in these areas, resulting in lower capture rates of these species. This exemplifies the fact that until variability in species specific responses are taken into account, patterns in community structure cannot be well understood.

2.4.3 Adjacent matrix restoration presents additional off-site ecosystem benefits

This study has provided evidence that the elimination of anthropogenic threats such as human encroachment, cattle grazing and frequent fires from the adjacent matrix can greatly determine the form and strength of edge responses of invertebrate communities. These results demonstrate that there is a strong influence of anthropogenic disturbances, such as cattle grazing and frequent fires, on the intensity of edge responses in dung beetle communities. In some cases, my results have even shown that pastoral species present in the regenerating matrix can be completely lost from degraded matrix habitats and many species that are almost extinct in degraded areas are persisting within areas of matrix restoration. Many studies have contributed to the convincing evidence for pervasive cross-ecosystem impacts that can penetrate far into natural habitat remnants (Didham et al. 1998, Laurance et al. 2002, Ewers and Didham 2008). Therefore, it has been suggested that these effects significantly decrease the effective reserve size (Laurance et al. 2011) supporting the argument that to mitigate these impacts, reserves need to be large and measures should be taken to reduce the effects of habitat edges by establishing regenerating buffers around forest reserves (Laurance 1991, Gascon et al. 2000).

This study shows that through a simple concerted restoration effort where zones of adjacent matrix habitat are protected from intensive cattle grazing and fires, this can lead to rapid and dramatic responses in invertebrate communities. Severe anthropogenic threats from intense land-use practices are highly common throughout Africa and much of the developing world where these processes often go unchecked and occur in close proximity to natural forest remnants (Hurault 1998, Oates 1999, Kotze and Samways 2001). With the backdrop of severe human land-use impacts in Afromontane forest systems, matrix habitat restoration adjacent to forest reserves presents great optimism for the conservation of dung beetle communities.

Chapter 3: Trait determinants of dung beetle species responses to land-use change

3.1 INTRODUCTION

Land-use change is the most important driver of population decline and loss of species worldwide (Tilman et al. 1994, Harrison and Bruna 1999, Sala et al. 2000, Foley et al. 2005). The resulting patterns (and processes) of biodiversity loss and community change are patently non-random, with some species clearly more affected than others (Henle et al. 2004, Ewers and Didham 2006a). This raises the question of whether the large variability observed in species responses to land-use change is simply unpredictable, or whether there might be certain species traits that can explain generalised patterns of species responses to global environmental change. In an attempt to move beyond this apparent idiosyncrasy of species responses and develop a more predictive understanding of which species are at greatest risk and why, research has more recently been targeted at the trait determinants of species sensitivity to environmental change.

Specific traits that have been identified as the most important determinants of species' sensitivity to environmental change include body size, dispersal ability, niche breadth, trophic level, and rarity (Henle et al. 2004, Ewers and Didham 2006a). For example, body size and fecundity were found to explain the large variation in extinction proneness across different avian families (Bennett and Owens 1997), whereas a study by Foufopoulos and Ives (1999) found habitat specialisation to be the strongest determinant of reptile extinctions under environmental change in the Mediterranean. However, Davies et al. (2000) found that rarity and trophic level explained extinction proneness better when looking at beetle species' responses to habitat fragmentation, and another study also found a strong effect of dispersal ability on beetle persistence in degraded landscapes (Driscoll and Weir 2005). These examples demonstrate that traits can be effective predictors of species responses to environmental change, but that the most important explanatory variables differ markedly in different contexts.

Implicit in these arguments for specific trait-determinants of species responses to disturbance is the concept that removal of these threatening processes through conservation management and habitat restoration will lead to the re-establishment of those species that were initially most affected. More precisely, the inference is that the trait determinants of community disassembly should be the same determinants of species recovery following the exclusion of threatening processes. However, to my knowledge this inference has never been tested.

A growing focus in restoration ecology has been to identify trait determinants of community reassembly to better understand the potential trajectories of restoration efforts (Funk et al. 2008). For example, Kirkman et al. (2004) found that dispersal limitation in ground-cover flora was a strong determinant of species recolonisation. Additionally, a study by Summerville et al. (2006) demonstrated that Lepidopteran flight behaviour and feeding preference predicted the propensity for species to recolonise disturbed prairie lands. These examples support the possibility of utilising trait-based theory to predict potential restoration outcomes for community composition. However, most studies attempting to quantify trait-determinants of community responses to environmental change tend to assume a fixed-trait perspective. That is, overall trait values are calculated from a subsample of individuals and extrapolated to the entire species across all geographical contexts and are then used to explain variability in species' responses to environmental change (e.g. Gibb et al. 2006, Lebrija-Trejos et al. 2010, Williams et al. 2010, Diamond et al. 2011, Pakeman 2011). As a result, there has been high variability across studies in identifying which traits are important determinants of species responses to anthropogenic disturbances.

The large amount of variability in the apparent significance of certain traits as determinants of species responses may be attributed to phenotypic variability within species and individual level trait plasticity. Phenotypic variation within species has been shown to increase more dramatically in response to "anthropogenic" selection pressures with the potential for large and rapid shifts in trait expression within species in an ecological timescale (Carroll et al. 2007, Hendry et al. 2008). Such significant phenotypic variability within species in anthropogenic landscapes has almost certainly led to contradictory findings and may continue to prevent the development of a common predictive framework for trait determinants of community assembly (Webb et al. 2010). Therefore, for the advancement of trait-based research in community responses to global environmental change, studies should take into account trait measurements at the individual level across populations in order to accurately quantify trait distributions at a community scale (Messier et al. 2010, Webb et al. 2010).

Invertebrate populations arguably present some of the most striking examples of trait variation and phenotypic plasticity of any taxa (Nylin and Gotthard 1998, Carroll 2007, Chown and Gaston 2010). This is exemplified in many examples such as the extremely rapid response of insect pest populations to insecticide in agroecosystems. Studies looking at pest resistance to agrochemicals have demonstrated significant variation in morphological and life-history traits, such as longevity and wing morphology, as a result of both evolutionary and plastic responses (McKenzie and Batterham 1994, Hoffmann et al. 2002). Other anthropogenic processes are also likely to drive shifts in insect species traits. For example Scharf et al. (2009) demonstrated that the degree of plasticity of Neuropteran morphology differed between wing loading and body size but both measures were found to respond strongly to climatic changes. Additionally, Parker et al. (2010) demonstrated remarkable evolutionary responses over ecological time scales in honey bees to climate variation as a result of human facilitated global introductions. Equally striking phenotypic variation has also been documented in insect populations in response to anthropogenic habitat degradation. For example, butterflies have been found to vary markedly in life-history traits (Karlsson and Van Dyck 2005) and dispersal power (Norberg and Leimar 2002) as forest fragmentation acts as a strong ecological filter by selecting for specific traits (Webb et al. 2010).

Despite the overwhelming evidence for high phenotypic variability and plasticity in invertebrate species, there is little knowledge of whether this within-species variability might mask (or perhaps even drive) variation in species-level responses to global environmental change. The aim of this study is to identify key morphological trait ‘mediators’ of community structural responses to edge effects and adjacent matrix restoration. To test these questions, I used dung beetle communities in a severely degraded Nigerian Afromontane landscape as a focal system. Dung beetles are an ideal invertebrate group for studying trait-dependent community responses to anthropogenic land-use change due to their high abundance, diversity, and variance in traits (Nichols et al. 2007, Larsen et al. 2008). Additionally, dung beetles are especially sensitive to anthropogenic disturbances and respond very rapidly to environmental changes, thus increasing the likelihood of detecting clear responses to environmental change (Klein 1989, Davis et al. 2001, Nichols et al. 2007). Therefore, this taxonomic group is ideal for identifying the role of individual trait plasticity in shaping species-level responses in trait composition to anthropogenic threats.

3.2 METHODS

3.2.1 Study design

The study was conducted in Afromontane forest at Ngel Nyaki forest reserve, located on the Mambilla Plateau near the south-eastern border of Nigeria (for a detailed description of the study site see Chapter 2). To quantify trait-dependence in dung beetle species responses to matrix restoration, I measured variation in the capture rates of dung beetle species along three replicate edge gradients in both degraded sites and regenerating sites (six sites in total), and tested the degree of association between species responses and species traits. Degraded sites were located in areas that were fully exposed to anthropogenic threats (such as intensive cattle grazing and fires), compared to the regenerating sites that were located in areas where these threats were entirely excluded for two to three years. Each replicate edge gradient consisted of 13 sampling points at fixed distances from the edge on a doubling scale from the forest to grassland matrix habitat (-160, -80, -40, -20, -10, -5, 0, 5, 10, 20, 40, 80, and 160 meters from the edge, where negative values represent forest samples) (see Chapter 2 for full experimental design). Traps were placed no closer than 50 meters apart in order to maintain independence between traps, as this distance is just beyond that over which dung beetles can detect dung (Larsen and Forsyth 2005). This method of trap placement therefore controlled for potential sampling bias from trap interference and spatial autocorrelation (Baker and Barmuta 2006).

3.2.2 Sampling, sorting, and identification of dung beetles

All sampling of dung beetle communities was conducted at Ngel Nyaki forest during the late rainy season from October 4th to November 29th 2009. I used pig dung-baited pitfall traps (see Chapter 2 for trap design) placed at each distance across the edge gradient for two consecutive 24 hour periods (i.e. two samples pooled into one 48 hour sample). All dung beetles in the subfamily Scarabaeinae were sorted to genus and assigned to initial ‘morphospecies’ groupings based on consistent morphological traits. Formal species identification was then undertaken by Rowan Emberson at the Lincoln University entomology collection and Frank Krell at the Denver Natural History Museum. For detailed sampling methods see chapter 2.

3.2.3 Measurement of individual specimen traits

To quantify variation in functional-trait dispersion and trait means between communities along regenerating and degraded edge gradients, five morphological traits were measured for individual dung beetle specimens within each species: body mass, body size, body condition index, wing area and wing loading, as described in detail below.

In order to facilitate trait measurements, individuals from each species in each pitfall sample were pinned using standard stainless steel (#2) entomological pins. All pins were individually pre-weighed for each beetle specimen to the nearest 0.001 mg using a Mettler Toledo UMX2 ultrafine microbalance. The absolute range of variation in pin mass was 4.029 mg (45.970 – 49.999 mg), which far exceeded the mass of the smallest beetle specimen (0.227 mg). For any given trap sample, all individuals were pinned for species that were represented by less than 20 individuals (in that sample), but for logistical reasons this was not possible for very abundant species that had more than 20 individuals (in that sample). For these abundant species, a random subsampling procedure was employed to reduce the number of individuals pinned. I placed all individuals of the abundant species into a Petri dish marked with eight equal radiating segments, and spread them approximately evenly across the dish. Each segment was assigned a number from one to eight and a random number generator was used to pick a segment from which to subsample beetles. All individuals in that segment were pinned and measured. If the total number of beetles from the first randomly-drawn segment was less than 20, all beetles in the next segment in a clockwise direction were also pinned and measured, and so on until more than 20 individuals were obtained. The nature of the subsampling procedure meant that often substantially more than 20 beetles were pinned from some very abundant species in some trap samples.

3.2.3.1 *Component traits: wing area, pronotum width, and body mass*

Immediately after pinning, when specimens were still moist and flexible, the left hind wing of each specimen was removed for morphometric analysis using fine forceps. The wing was then mounted and spread open on a microscope slide using glycerine jelly with 2 % phenol as a preserving agent. This mounting agent solidifies at room temperature, therefore the slide was kept warm on a heating element while the wing was being mounted, and was then cooled immediately after a coverslip had been placed over the wing. Subsequently, a digital image was taken of each wing using a Nikon D40 SLR camera with a macro lens, mounted at a fixed height directly above the slide. A 1 cm scale bar was placed next to the slide-mounted beetle wing in order to calibrate wing measurements.

Digital images were processed using Adobe Photoshop CS2 in order to obtain a measure of wing area. This was achieved by digitally clipping out the wing from the image background and then digitally filling in the wing area with black on a white background. In order to standardise the point at which each wing was cut at the base, all images were clipped in a plane bisecting homologous vein junctions, as shown in Figure 3.1. The image file was then saved as a bitmap and imported into Image J software to calculate total image area from the scale bar, and proportion of total area represented by black pixels. This gave wing area in mm^2 for one wing which was then multiplied by two for an approximation of absolute wing area per beetle.

Figure 3.1 Example of the left hind wing of an individual male *Onthophagus* sp.1. Red arrows mark the two vein juncture landmarks used to orient a planar cut off point (black dashed line) for standardisation of area measurements.

Body size was measured using the width of the pronotum as a simple linear surrogate of overall size. This measure was the most suitable because other measures such as body length can vary idiosyncratically in beetles due to the expansion or contraction of the soft tissues at arthrodial joints. Furthermore, pronotum width in dung beetles has been found to be positively correlated with female reproductive output and mating success in males (McLain 1991, Hunt and Simmons 2001, Kotiaho et al. 2003) and is therefore a useful indirect measure of beetle fitness.

Once individuals were pinned, and the left wing was removed, they were stored in a cool, dark room for a minimum of four months to air-dry. Specimens smaller than 300 mg were put in a drying oven at 60 °C for two hours to achieve complete drying and immediately weighed to the nearest 0.001 mg as described above. The required drying time was established by repeatedly re-weighing a test set of beetles in the drying oven until the specimens reached a constant mass. For all specimens larger than 300 mg, individual drying times were continued beyond two hours at 60° C, until each specimen reached a constant mass. The mass of each beetle was then calculated by subtracting the pre-recorded mass of that individual pin from the total mass of the beetle plus pin after drying. For trap samples in which some individuals of abundant species were not pinned (i.e. were not in the subsample selected for pinning), the total mass per abundant species was calculated from the mean measured mass of individuals of that species in that particular sample and multiplied by the total number of individuals of that species found in that sample. Across species, these estimates were then used to calculate total dung beetle mass per trap sample.

3.2.3.2 *Aggregate traits: body condition index and wing loading*

A body condition score was calculated as body mass divided by body size which can be used as a surrogate for individual fitness. Kotiaho et al. (2001) broadly referred to condition as the pool of internal resources available for utilisation. In this study I use this definition as a body condition index whereby condition = body mass (mg)/pronotum width (mm), giving a more comprehensive and direct measure of available resources (i.e. fat stores, food, eggs, etc.) between beetles than pronotum width alone.

Wing loading was calculated as absolute wing area divided by body mass (Dudley 2000). While absolute wing area explains some dispersal characteristics in insects, wing loading provides a more comprehensive measure as it incorporates effects of variation in muscle mass and load, which also determine flight capacity (Dudley 2000, Berwaerts et al. 2002). As removal of one wing of each specimen to measure wing area inherently reduces measured total body mass, my wing loading calculation will be a slight underestimate in all cases. However, I assume that the degree of underestimation will be randomly distributed and consistent across treatments.

3.2.4 Statistical Analysis

3.2.4.1 *Species responses to degraded and regenerating forest edges*

Continuous edge response functions were quantified for the relative capture rates of individual dung beetle species across patch-to-matrix gradients for each of the two levels of habitat edge condition (degraded and regenerating), using the statistical approach of Ewers & Didham (2006b). Using a form of the general logistic model, I determined the best-fit edge model out of five models of increasing complexity (Ewers and Didham 2006). For specific model fitting methods see chapter 2. Edge response functions were only determined for species that had more than $n \geq 13$ individuals captured in total (i.e. species sufficiently abundant to have the potential to be distributed across all 13 distances from edge).

3.2.4.2 *Trait determinants of species responses*

First, I tested for the potential trait determinants of species' responses to edge effects at degraded forest edges. To do so, I conducted multiple regression models with species' trait means as predictors and species' sensitivity to edge effects as response variables. I used edge magnitude (the disparity in relative capture rates between matrix and forest habitat) and edge extent (the spatial distance over which edge responses can be detected). Edge extent was approximated by the number of sampling distances (out of 39) that species were absent across all degraded edge gradient sites (Larsen et al. 2008) and analysed using a logistic generalised linear model with quasi-likelihood distribution (to account for overdispersion). Analysis of the trait determinants of species responses was only conducted for species that were sufficiently abundant ($n \geq 13$).

Second, in order to test the potential trait determinants of species responses to matrix restoration, I ran a multiple regression with trait means for each species as predictors and species' sensitivity to matrix restoration as the response. This was done by developing two measures that reflected differential responses of species between edge gradient treatments (i.e. degraded and regenerating sites). Firstly, I measured the difference between degraded and regenerating sites in proportion of all samples in which species were present (i.e. species distribution). This measure gives an approximation of the difference in the extent of edge effects between the two land-use treatments. Secondly, I quantified the difference in the magnitude of edge response between degraded and regenerating edge response functions of individual species. In contrast to the first measure, change in edge magnitude gives a measure of the disparity in relative capture rates of species along the edge gradient (Ewers and Didham 2006b). These values were then used as response vectors in multiple regression models in the R environment. To determine the trait means that best predicted variation in species responses to matrix regeneration, I used AIC (Akaike information criterion) scores for maximum likelihood model selection to determine the model of best fit.

3.2.4.3 *Testing for a community-wide shift in trait means and functional trait dispersion*

In order to determine if trait-mediated effects on species' distributional responses were strong enough to drive a shift in community trait means, I quantified continuous edge response functions for trait means of each community between degraded and regenerating matrix edge gradients. Furthermore to test if habitat degradation or regeneration near forest edges resulted in a community-wide shift in functional trait dispersion, I calculated a distance-based metric of trait dispersion 'FDis' (Functional Dispersion) using the "FD" package in the R language environment (Laliberte and Legendre 2010). The FDis metric takes into account multiple trait characteristics of organisms within a community and measures the distance of each species to the trait-mean centroid of the whole community. It is a multivariate adaptation of weighted mean absolute deviation, where the weighting is given by the relative abundance of species (Laliberte and Legendre 2010), and is thus a weighted measure of trait variation or complementarity among species in a given community. To calculate FDis, I first compiled a trait matrix with mean trait values for each species, then calculated Gower dissimilarity coefficients among species trait complexes using the "gowdis" function. This was used to determine multivariate dispersion of assemblages based on the Gower dissimilarity coefficients weighted by species' relative abundances. I tested whether functional dispersion varied significantly over patch-to-matrix edge gradients in degraded versus regenerating sites using the statistical approach to fitting continuous edge response functions described above.

3.2.4.4 *Trait-plasticity in response to edge effects and matrix restoration*

To determine levels of species' trait plasticity, continuous edge response functions were used to quantify variability in the distribution of traits within species. Forest-to-matrix edge response functions were compared between degraded and regenerating sites. This analysis was carried out on the 13 most abundant species of which there were ≥13 individuals, using the statistical approach described above for fitting continuous edge response functions.

3.3 RESULTS

3.3.1 Dung beetle responses to forest regeneration are highly variable among species

A total of 4705 dung beetles comprising 35 species in 11 genera were captured across all sites. In total, 3045 individuals were subsampled for the measurement of morphological traits (Table 3.1). A high level of variation was found in trait values among species with greater than three orders of magnitude change in mean body mass across species.

Species-level analyses of relative capture rates revealed that, across the 13 species that provided sufficient numbers for testing edge response functions, 12 out of the 13 species responded significantly to edges. Among these 12 species, clearly defined habitat preferences were revealed (i.e. forest, edge, or matrix habitat preference) with high variability in edge response functions (Figure 3.2). Of particular interest were the differences between regenerating and degraded edge responses among species (Figure 3.2) where 83% of the 12 species that responded significantly to edge effects had significantly different response magnitudes between the degraded and regenerating edge gradients.

Table 3.1 Dung beetle species collected with their respective trait values and number of individuals captured. Trait values are the arithmetic mean for each species calculated from all measured individuals and extrapolated to the total collection (all but two singleton species that were damaged). BCI (body condition index) = body mass / pronotum width. Wing loading = body mass / wing area. Values under 'Individuals measured' are given as number of subsampled specimens out of the total number of individuals in parentheses.

Species	Body mass (mg)	Pronotum width (mm)	Wing loading	BCI	Individuals measured
Caccobius sp.1	1.197	2.053	0.083	0.579	4 (4)
Caccobius sp.2	1.159	2.031	0.122	0.571	1 (1)
Catharsius dux	702.938	18.940	0.708	37.040	4 (5)
Catharsius sp.2	78.211	9.566	0.257	8.175	3 (3)
Catharsius sesostris	136.363	12.274	0.291	11.110	1 (1)
Diastellopalpus nigerimus	226.960	12.089	0.987	18.627	64 (64)
Latidrepanus caelatus	2.786	2.528	0.192	1.098	40 (40)
Heliocopris myrmidon	1543.067	25.725	0.850	59.868	3 (3)
Liatongus arrowi	15.674	4.503	0.376	3.481	1 (1)
Neosisyphus armatus	19.178	4.636	0.459	4.095	4 (4)
Onitis sp.1	214.119	12.786	0.844	16.680	10 (10)
Onitis sp.2	133.414	10.596	0.838	12.591	1 (1)
Onthophagus sp.1	29.861	6.022	0.342	4.920	181 (181)
Onthophagus sp.2	7.737	3.615	0.237	2.122	1176 (2013)
Onthophagus sp.3	2.910	2.757	0.161	1.058	1006 (1787)
Onthophagus sp.4	3.018	2.715	0.107	1.111	4 (4)
Onthophagus sp.5	2.597	2.529	0.192	1.005	22 (22)
Onthophagus sp.6	2.172	2.468	0.145	0.871	118 (161)
Onthophagus sp.7	5.187	3.048	0.161	1.666	23 (23)
Onthophagus sp.8	10.681	3.885	0.293	2.706	18 (18)
Onthophagus juvencus	7.928	3.656	0.222	2.167	5 (5)
Onthophagus alternans	3.866	3.204	0.190	1.206	14 (14)
Onthophagus sp.11	0.447	2.958	0.026	0.176	2 (2)
Onthophagus rufonotatus	21.990	4.989	0.552	4.385	4 (4)
Onthophagus sp.13	3.850	2.905	0.196	1.318	30 (30)
Onthophagus sp.14	3.087	2.723	0.202	1.132	6 (6)
Onthophagus sp.15	11.207	4.478	0.169	2.508	7 (7)
Onthophagus sp.16	11.220	3.777	0.390	2.949	9 (9)
Onthophagus sp.18	2.089	2.561	0.147	0.816	1 (1)
Onthophagus sp.19	1.453	2.693	0.087	0.541	2 (2)
Onthophagus sp.21	3.660	4.062	0.086	0.901	1 (1)
Proagoderus elgoni	53.673	7.702	0.627	6.829	13 (13)
Proagoderus multicornis	60.012	7.895	0.564	7.512	9 (9)
Sisyphus sp.1	2.740	2.720	0.167	1.000	30 (30)

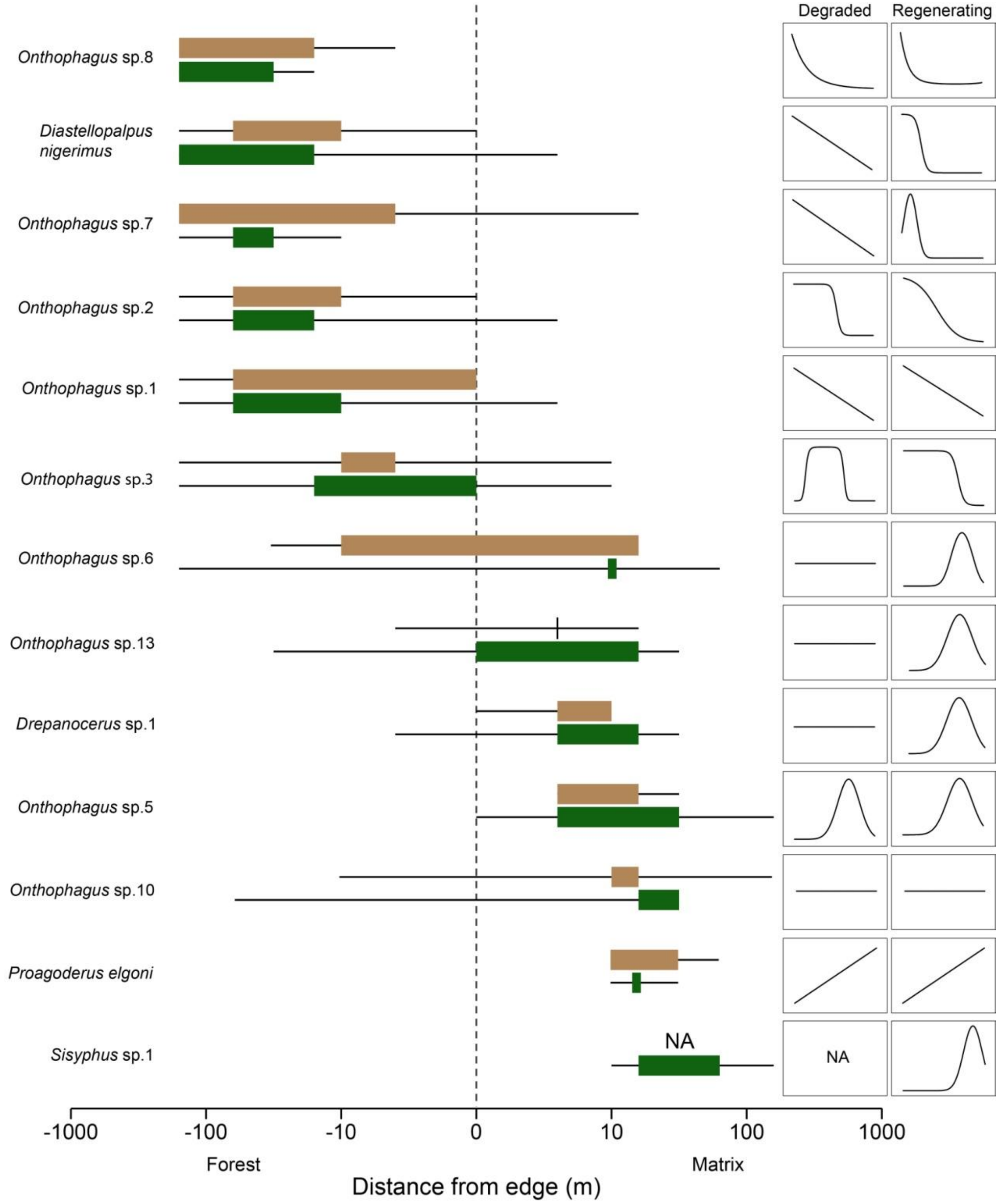


Figure 3.2 Spatial distribution of dung beetle occurrences at degraded (brown) versus regenerating (green) edges, for the 13 most abundant species (N ≥ 13). Thick coloured bars indicate the interquartile range of species' abundances, and thin horizontal lines indicate distributional range in relation to distance from forest edge. Negative values on the x-axis indicate forest sites. Thumbnail graphs to the right display statistically fitted edge response functions for capture rates of each species at degraded and regenerating edges. NA indicates no species occurrence.

3.3.2 Variability in species responses are partially explained by species trait means

Regression analyses revealed that the relative distributions of species (proportion of samples that a given species was absent from) across degraded edge gradient were not explained by species traits (n = 13, $P > 0.05$ for all trait predictors). Likewise, species traits were not found to significantly determine magnitude of edge responses of species in degraded habitats (n = 13, $P > 0.05$ for all trait predictors).

Analysis of trait determinants of species responses to habitat regeneration found that the difference in magnitude of edge response functions between degraded and regenerating edge gradients were not explained by variation within species' traits (n = 13, $P > 0.05$). However, species' trait means were found to determine differences in edge extent (the distribution of species across edge sampling distances) between degraded and regenerating edge gradients. In particular, wing loading had a negative effect on distributional differences in species between levels of matrix condition, whereby species with lower wing loading were found more frequently in regenerating sites ($F_{2, 10} = 17.88$, $P < 0.01$). In contrast, I found a positive effect of body condition index (BCI) on the difference in species distributions ($F_{2, 10} = 16.51$, $P < 0.01$) whereby beetles with a low BCI were found to be more evenly distributed across all habitats compared to beetles with high BCI.

3.3.3 Habitat regeneration drives a community-wide shift in traits across edges

Despite only limited evidence of species-level trait determinants of variation in the edge response functions of individual species across degraded and regenerating edges, there were highly-significant shifts in community-level weighted trait mean values across edges for all dung beetle traits measured (Table 3.2). Perhaps the most striking response was the large difference in edge response functions in community-weight trait values between the degraded and regenerating habitat edge gradients. Community weighted trait means varied in opposite directions across the forest-to-matrix habitats depending on adjacent matrix restoration (Figure 3.3). Community means for body mass, pronotum width, wing loading, and body condition index all significantly decreased from forest to regenerating matrix habitat, compared to degraded edge communities which displayed substantially higher community-weighted trait mean values in the matrix (Figure 3.3).

Table 3.2 AIC scores obtained from the edge function fitting procedure for models of increasing complexity (null, linear, exponential, logistic, and unimodal) for both degraded and regenerating edge gradients. Response codes stand for functional dispersion (FDis), body mass (BM), pronotum width (PW), wing loading (WL), and body condition index (BCI). AIC scores in bold indicate model of best fit for a given response.

	Degraded					**Regenerating**				
	Null	Linear	Exponential	Logistic	Unimodal	Null	Linear	Exponential	Logistic	Unimodal
Community										
BM	1326.96	1328.096	NA	1171.268	**1161.62**	2816.973	**2342.004**	NA	NA	2306.426
PW	5672.508	5641.298	NA	**5377.515**	5505.456	11287.06	11089.97	NA	**11052.37**	11052.85
WL	-1941.59	-1956.63	NA	**-2111.8**	-2054.17	-3844.75	**-3952.66**	NA	NA	NA
BCI	7463.268	7418.689	NA	**7220.919**	NA	15176.13	15089.51	NA	**15064.11**	15081.93
FDis	-92.724	-93.43	NA	NA	**-98.333**	**-144.615**	-143.342	NA	NA	NA
***Onthophagus* sp.1**										
BM	-43.546	**-45.904**	NA	NA	NA	**-166.664**	-166.628	NA	-166.389	NA
PW	60.425	**58.697**	NA	NA	58.992	201.119	**195.631**	197.642	198.488	NA
WL	**-74.248**	-73.581	NA	NA	NA	**-286.841**	-284.875	NA	NA	NA
BCI	170.605	**168.953**	NA	171.114	NA	**421.699**	422.848	NA	NA	424.75
***Onthophagus* sp.2**										
BM	-993.966	-1015.88	NA	**-1057.04**	-1056.22	**-1802.28**	-1802.4	NA	NA	NA
PW	**-129.978**	-127.981	NA	NA	-126.018	**276.643**	276.864	NA	NA	NA
WL	-1817.73	**-1838.67**	NA	NA	NA	-3828.51	-3837.5	NA	NA	**-3840.29**
BCI	955.973	929.653	NA	**886.293**	888.951	2183.082	2183.582	NA	NA	**2180.021**
***Onthophagus* sp.3**										
BM	-1486.62	**-1490.23**	NA	NA	NA	-2613.76	**-2616.03**	NA	NA	NA
PW	**-397.617**	-397.397	NA	NA	NA	**394.417**	393.768	395.768	NA	NA
WL	**-2677.4**	-2677.4	NA	NA	NA	**316.968**	318.917	317.696	NA	NA
BCI	-220.971	**-223.177**	NA	NA	NA	-4592.34	**-4601.22**	NA	NA	NA
***Onthophagus* sp.5**										
BM	**0.762**	NA	NA	NA	NA	**-0.69**	-0.137	1.803	3.803	1.816

PW	**5.233**	7.11	8.637	NA	NA	5.626	**4.546**	6.55	8.053	6.075
WL	**-13.666**	-11.666	NA	NA	NA	**-31.891**	-31.094	-29.233	NA	-29.257
BCI	**8.216**	10.212	NA	13.72	NA	**20.234**	20.404	NA	24.354	22.357
***Onthophagus* sp.6**										
BM	**-10.423**	-9.132	-7.132	NA	NA	**-233.128**	-231.213	NA	NA	-229.809
PW	-7.161	**-9.208**	-7.969	NA	NA	**-66.563**	-64.763	NA	NA	NA
WL	-26.508	**-29.452**	NA	NA	NA	**-515.103**	-513.107	NA	NA	NA
BCI	**5.857**	6.69	8.691	NA	NA	**40.898**	42.759	NA	NA	43.72
***Onthophagus* sp. 7**										
BM	NA	NA	NA	NA	NA	**2.935**	4.67	5.884	NA	6.362
PW	NA	NA	NA	NA	NA	**8.692**	10.428	12.428	NA	12.283
WL	NA	NA	NA	NA	NA	**-36.687**	-34.73	-33.037	NA	-32.865
BCI	NA	NA	NA	NA	NA	**42.032**	43.894	45.301	NA	45.579
***Onthophagus* sp. 8**										
BM	**-4.018**	-2.037	NA	NA	-0.647	-26.508	**-29.452**	NA	NA	NA
PW	**14.547**	16.207	17.355	NA	18.021	**10.267**	11.652	NA	NA	11.567
WL	**-21.867**	-19.87	-19.846	NA	-18.529	**-24.746**	-24.133	NA	NA	NA
BCI	**24.506**	26.288	25.571	NA	27.425	**14.559**	16.342	NA	NA	NA
***Onthophagus* sp. 10**										
BM	-12.326	**-18.875**	NA	NA	NA	NA	NA	NA	NA	NA
PW	**-8.48**	-6.652	NA	NA	NA	NA	NA	NA	NA	NA
WL	-31.75	**-37.639**	NA	NA	NA	NA	NA	NA	NA	NA
BCI	1.188	**-7.305**	NA	NA	NA	NA	NA	NA	NA	NA
***Onthophagus* sp.13**										
BM	NA	NA	NA	NA	NA	**-55.8**	-54.406	-52.406	NA	-52.812
PW	NA	NA	NA	NA	NA	**-12.353**	-10.643	NA	-6.743	NA
WL	NA	NA	NA	NA	NA	-108.017	**-109.211**	-107.211	NA	NA
BCI	NA	NA	NA	NA	NA	**-9.511**	-9.391	-7.389	NA	NA
Diastellopalpus nigerimus										
BM	**-22.814**	-22.452	NA	-21.273	-23.141	**-83.482**	-84.057	NA	-82.436	-84.023
PW	**36.17**	38.168	NA	NA	36.864	**141.204**	140.562	NA	144.328	NA

WL	**-13.112**	-12.267	NA	-9.871	-12.187	**-43.723**	-42.026	NA	NA	-42.854
BCI	66.077	**64.656**	NA	65.615	NA	**266.667**	266.978	269.009	267.966	NA
***Drepanocerus* sp.1**										
BM	NA	NA	NA	NA	NA	**-23.914**	-21.975	NA	NA	-20.091
PW	NA	NA	NA	NA	NA	**-16.551**	-15.502	NA	NA	-14.854
WL	NA	NA	NA	NA	NA	**-115.824**	-114.478	NA	-110.677	-112.676
BCI	NA	NA	NA	NA	NA	**9.791**	11.625	NA	NA	NA
Proagoderus elgoni										
BM	NA	NA	NA	NA	NA	**-3.184**	-2.641	NA	NA	NA
PW	NA	NA	NA	NA	NA	**19.442**	19.394	NA	NA	NA
WL	NA	NA	NA	NA	NA	**-7.822**	-6.267	NA	NA	NA
BCI	NA	NA	NA	NA	NA	**23.302**	24.207	26.208	NA	NA
***Sisyphus* sp.1**										
BM	NA	NA	NA	NA	NA	**-6.509**	-4.647	-2.665	NA	-2.81
PW	NA	NA	NA	NA	NA	**-7.253**	-7.755	-7.358	NA	-7.491
WL	NA	NA	NA	NA	NA	**-71.285**	-69.309	-67.836	NA	NA
BCI	NA	NA	NA	NA	NA	**31.645**	33.642	35.642	NA	NA

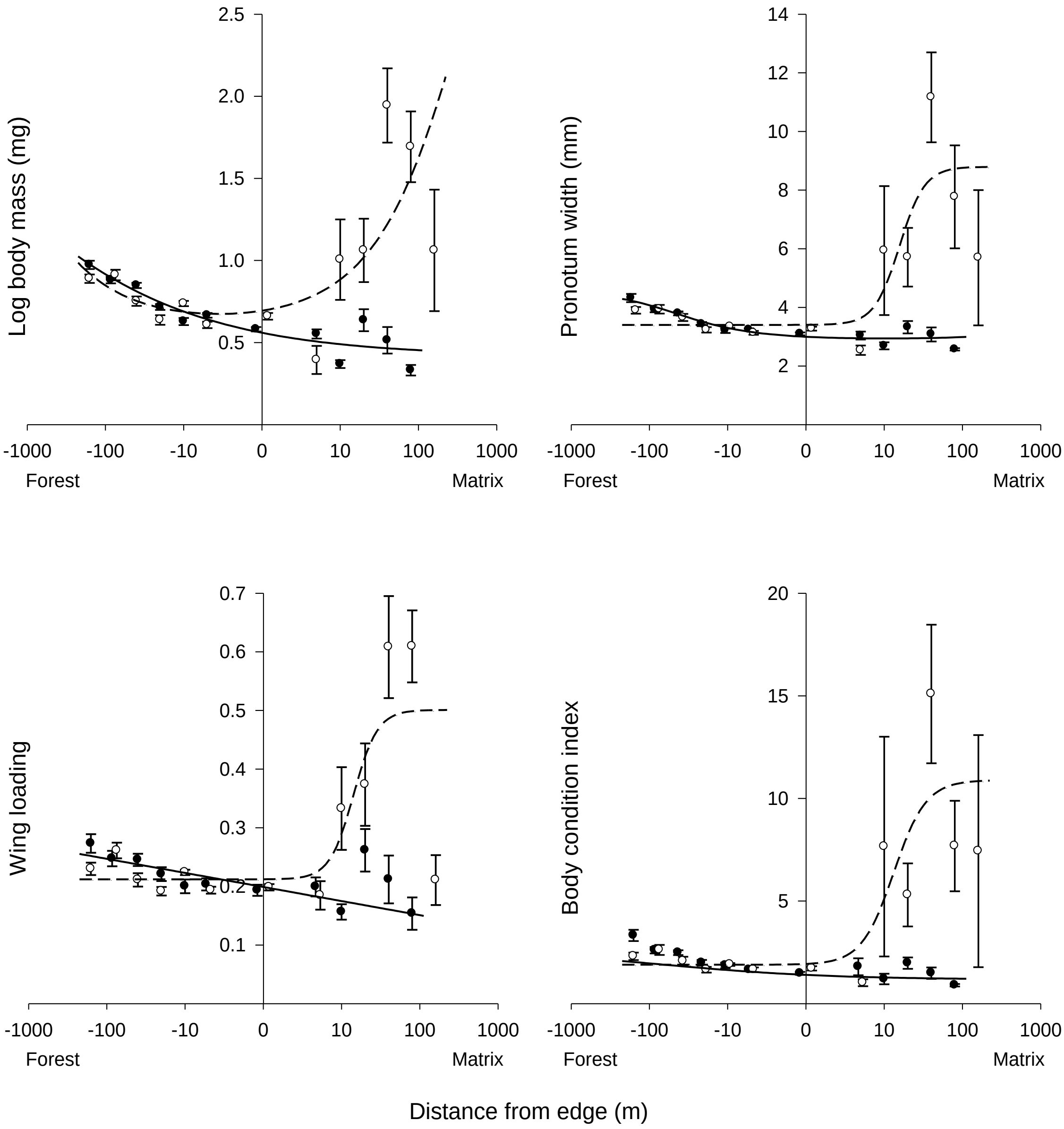


Figure 3.3 Variation in community-weighted mean (± 1 SE) trait values for all dung beetle species (combined), across degraded (open symbols and dashed fitted lines) versus regenerating (closed symbols and solid fitted lines) edge gradients. Negative values on the x-axis indicate forest sites. Lines are the best-fit continuous edge response functions of five fitted models of increasing complexity. Overlapping data points are offset for clarity.

Community-wide functional trait dispersion also differed significantly between degraded and regenerating edge gradients. Degraded habitat edges were found to have significantly higher community-wide trait dispersion in degraded matrix sites, whereas the functional dispersion of dung beetle communities did not differ significantly between forest and regenerating matrix sites following matrix restoration (Figure 3.4).

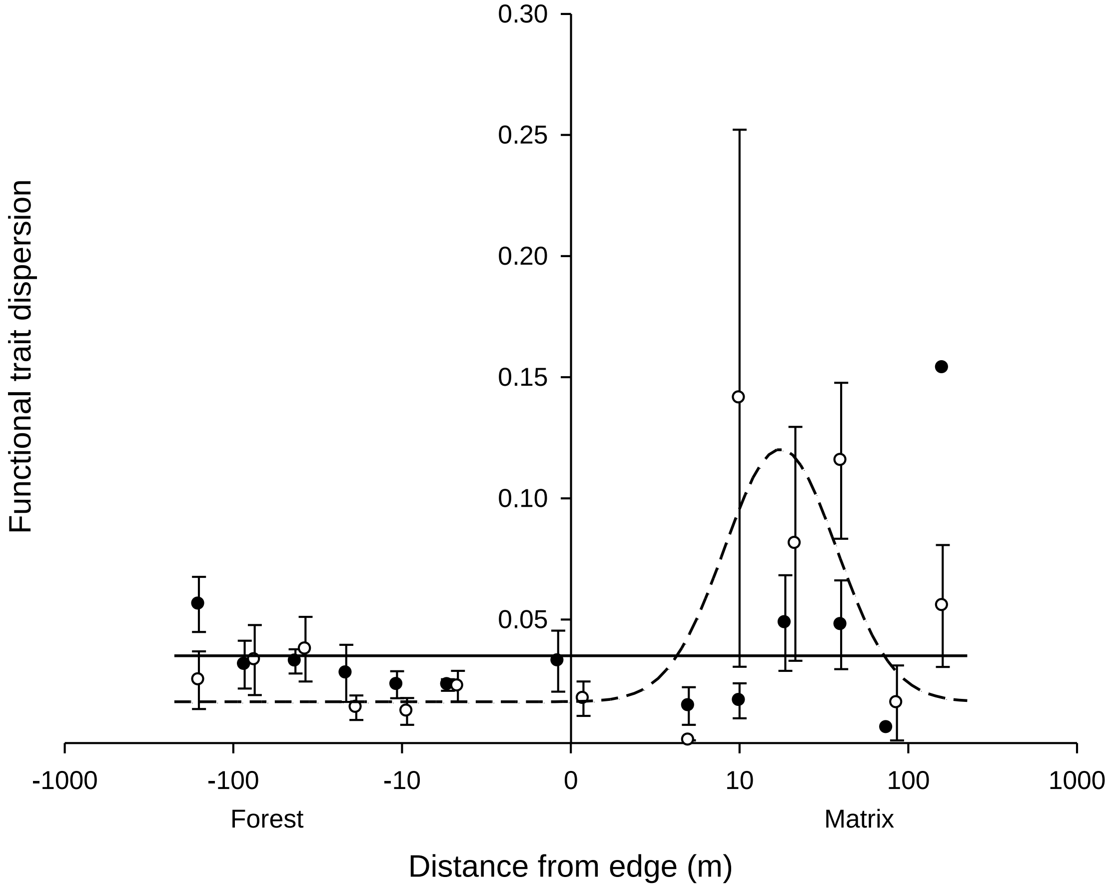


Figure 3.4 Variation in community-weighted mean (± 1 SE) functional dispersion (FDis) of dung beetle communities across degraded and regenerating edge gradients. Symbols and lines as in Figure 2. Overlapping points are offset for clarity.

3.3.4 Environmental change drives within-species trait plasticity

Of the 13 species that were selected for analyses (species with ≥13 individuals), nine displayed significant within-species variation in trait values across patch-to-matrix edge gradients for at least one or more of the four morphological traits measured. Distributions of body mass, pronotum width, wing loading, and body condition index values within species showed significant responses to edges depending on the species measured. For example, in 5 of the 13 species there was significant variability across habitat edges in body mass and BCI, and in 4 out of the 13 species there was significant variation in pronotum width and wing loading.

Moreover, there were large differences in within-species trait values between degraded and regenerating edge gradients (Table 3.2). Seven out of the 13 most abundant species had a sufficient number of individuals across both matrix treatments so that degraded vs. regenerating habitat comparisons could be made for within-species trait differentiation. Six of these seven species exhibited significant differences in within-species trait distributions at degraded versus regenerating edges (Table 3.2). This is clearly demonstrated by the most abundant species, *Onthophagus* sp.2, in which response functions fitted for trait distributions differed significantly between levels of matrix degradation (Figure 3.5).

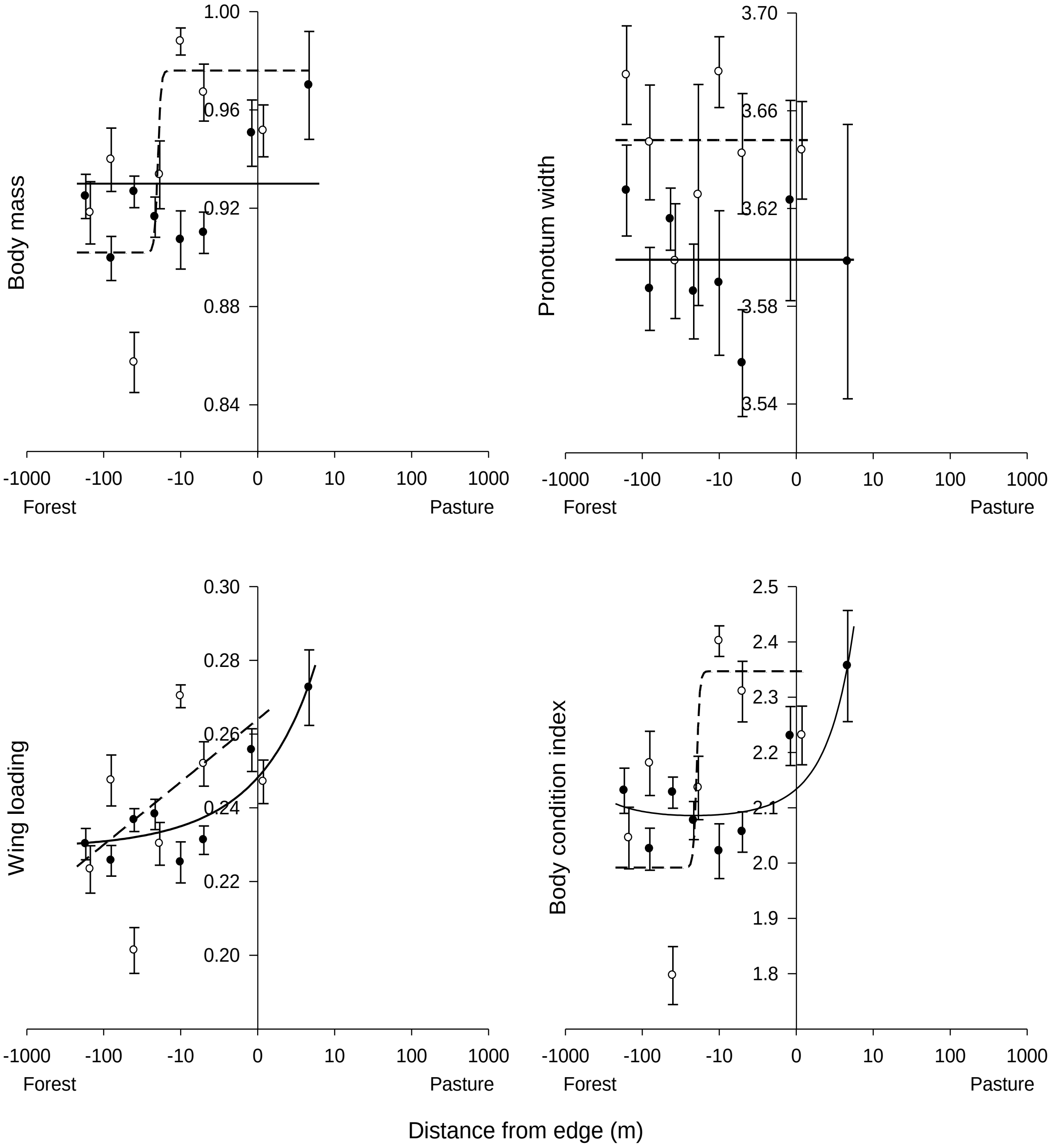


Figure 3.5. Variation in mean (± SE) trait values of *Onthophagus* sp.2 across degraded (open symbols and dashed fitted lines) versus regenerating (closed symbols and solid fitted lines) edge gradients. Fitted lines as in Figure 2. Negative values in the x-axis indicate forest sites and overlapping points are offset for clarity.

3.4 DISCUSSION

Due to the high variability in species responses to environmental change, a better understanding of traits that potentially mediate these responses is central to developing a predictive framework for measuring and monitoring the impacts of global change drivers on community structure (Henle et al. 2004, Webb et al. 2010). My results show that dung beetle species exhibit large differences in their responses to edge effects and the condition of the adjacent matrix. In particular, I found that morphological traits were able to explain variation in the responses of species to the off-site effects of restoration of the adjacent matrix habitat, even though these same species-level traits were weak predictors of species responses to edge effects at degraded sites. This brings to light an important issue whereby trait means provide weak explanations of species distributions, despite the very strong ecological filtering of community-weighted trait distributions, resulting in a shift in functional-trait dispersion. This indicates that—as demonstrated by the within-species trait plasticity responses found in this study—species exhibit high trait variability between individuals. Therefore, through the dismissal of this variability, predictive power and accuracy in trait-based research can be lost.

3.4.1 Morphological traits predict responses in species distributions

Continuous edge response functions measured for individual species' relative capture rates show that there are remarkable differences in the way species respond to edge effects. These effects were also highly dependent on the restoration of the adjacent matrix habitat. This is a clear indication that specific differences in species' characteristics determine their relative sensitivity to the off-site impacts of adjacent matrix condition. Results from the regression analyses on species occurrences showed that species' trait means do not appear to explain the spatial distributions of species in the degraded habitats. However, morphological traits were good predictors of species responses to the regeneration of degraded adjacent matrix habitat.

In particular, species with lower wing loading were found to have larger differences in distributional range between degraded and regenerating edge gradient sites than species with higher wing loading. Increased wing loading is positively correlated with thoracic muscle mass per unit wing area and therefore often translates to increased flight and dispersal power in insects (Dudley 2000, Berwaerts et al. 2002).

Therefore, as 12 out of the 13 species tested showed broader spatial distributions and greater abundance in regenerating habitat, these results suggest that species with lower dispersal power (low wing loading) have higher persistence across regenerating than degraded habitats. On the other hand, beetles with high dispersal abilities are more likely to persist in degraded habitat where there are greater distances between suitable refuges within the matrix.

The positive effect of body condition index on the difference in distributions from degraded to regenerating habitat edge gradients indicates that high body condition of dung beetles appears to confer higher sensitivity to the restoration of the adjacent matrix habitat. Body condition index is potentially highly correlated with fitness measures such as muscle mass per unit area or fecundity (Kotiaho et al. 2001) but—as this trait has been used as an overall species measure to compare between species—in this case it can be interpreted as a consistent species morphological trait. While the use of overall species trait values in these regression analyses gives a clear indication of the presence of trait-mediated community assembly in dung beetles, these results do not express the exact nature of ecological trait filtering. In other words, to better understand the importance of traits for structuring communities, it is necessary to determine where certain traits are more or less common.

3.4.2 Edge effects drive responses in community-weighted trait distributions

In order to develop an explicit understanding of the role that species traits play in determining community responses to environmental change, trait variation needs to be measured at multiple levels of a stressor as this can explain how ecological filters are acting on specific traits and thus determining the structure of communities (Webb et al. 2010). In this study, the quantification of trait means from all individuals in each community revealed strong filtering effects of habitat edges on dung beetle trait composition. An especially striking result was the increase in magnitude change and difference in shape of edge functions in community trait means between degraded and regenerating habitat edge gradients. These results explicitly demonstrate that species traits are important determinants of the continuous responses of species to environmental change.

Across regenerating edge gradients I found a significant decrease in body mass, pronotum width, wing loading, and body condition index with increasing distance into the matrix. In contrast, while trait distributions responded similarly at degraded sites from the forest interior up to the edge, there was a significant increase in all four trait means within the degraded matrix habitat. Although the reasons remain speculative, these responses in trait composition are most likely explained by a combination of vegetative structure, resource availability, and climatic conditions. For example, larger dung beetles with higher wing loading are known to predominantly use a cruising flight foraging strategy whereby they remain airborne for longer periods of time until a dung pat is located, compared to perch-and-wait behaviour of smaller dung beetles in which they may wait in plant foliage until they detect dung nearby (Hanski and Cambefort 1991, Davis 1999). With this in mind, in areas of regenerating matrix habitat, where there are dense shrubs and grasses with much more complex habitat stratification, smaller dung beetles would be expected to persist compared to degraded matrix, which lacks complex vegetation. Lack of vegetation would prevent smaller beetles with lower wing loading from using perch-and-wait foraging strategies, thus selecting for beetles that use the cruising flight strategy. Additionally, microclimatic conditions in the degraded matrix would also present higher temperature extremes and lower humidity that smaller-bodied exothermic organisms would be less tolerant (Chown et al. 2002). Lower body mass and wing loading might be selected for at habitat edges where vegetative density is very high, whereas larger bodied species are likely to prefer deeper forest habitat as it is more open, allowing for a cruising flight strategy. On the other hand, the avoidance of regenerating matrix habitat by larger dung beetles might be explained by a lack of dung resources in the regenerating matrix habitats. Cattle exclusion was maintained in these habitats as a restoration effort and therefore these areas had much lower levels of dung deposition. Therefore, these regenerating habitats were unlikely to support the especially large dung beetle species found in the degraded matrix habitat.

Edge effects and the restoration of the adjacent matrix not only drove a community-wide shift in trait composition but also resulted in a shift in functional trait dispersion i.e. the divergence of traits within a community. Interestingly, functional dispersion was higher for communities in the degraded matrix habitat than those measured in both degraded and regenerating forest habitats. This response was most likely driven by the somewhat haphazard occurrence of very large bodied dung beetle species with high wing loading in the degraded matrix. As these beetles were rarely found anywhere else, their presence would have greatly increased the relative functional dispersion for a given community.

3.4.3 Within-species trait distributions scale up to community-level responses

Community-weighted trait means provide a valuable indication of distributional responses of traits to anthropogenic drivers of change as they take into account both among and within-species trait variation. However, to better understand the processes that drive patterns in trait distributions observed at the community level, we need to take into account selective mechanisms acting at different scales (Messier et al. 2010). This study has shown that dung beetle communities are subject to strong trait filtering mechanisms across continuous ecological gradients from the population to community level. Also, the strong responses in trait distributions within species indicate that these dung beetle species are subject to selective processes across relatively small spatial scales. Interestingly, body size in dung beetles is mostly determined by parental resource provisioning during larval development, as opposed to genetic inheritance (Hunt and Simmons 2002). This suggests that, in habitats where species exhibited a reduction in body size, these responses are most likely a result of constraints on resource acquisition by adult beetles from previous generations. This would in turn affect other morphological traits, such as wing loading, as thoracic muscle development would be largely determined by early development of body size through resource provisioning and could therefore have larger-scale impacts on species dispersal throughout communities.

In many cases, within-species trait distributions were found to differ considerably from community level trait distributions. This suggests that mechanisms driving trait selection at the population level differ from those acting at the community level. Within species, such mechanisms might be ontogenetic determinants of traits such as parental resource acquisition across different habitat quality determining body size in offspring. In contrast, at the community scale, random factors and interspecific species interactions may play a more important role in driving trait distributions across varying habitat quality. For example, fire disturbances in adjacent degraded matrix would most likely drive local extinctions of resident dung beetle populations in these areas. Therefore community assembly in these degraded habitats is likely to be driven by species with higher dispersal power that can quickly recolonise these disturbed habitats, thus selecting for beetles with higher wing loading. Additionally, recolonisation may simply occur via random processes such as the incidental close proximity of certain beetles at a given time. These processes are likely to explain the large degree of variability in community level trait distributions in the highly disturbed matrix in degraded habitats, compared with the relatively consistent variation observed in species level trait distributions.

3.4.4 Conclusions

This study shows that, not only do communities respond strongly to habitat degradation through changes in relative abundances and capture rates of species, but also in the trait structure of community composition. From these results, there is strong evidence for the trait-mediated reassembly of dung beetle communities across habitat edges that are adjacent to regenerating matrix. Therefore, these results demonstrate the efficacy of a trait-based approach for understanding the possible trajectories of community reassembly in restoration efforts.

Moreover, this study has also shown that through the restoration of adjacent matrix habitat, there are not only shifts in the taxonomic composition of dung beetle communities but also significant responses in the distribution of functional traits. As these traits determine the way in which beetles can utilise resources in their environment (de Bello et al. 2010), such a community-wide shift in functional traits has important implications for ecosystem functioning in degraded habitats.

Chapter 4: The importance of ‘response’ and ‘effect’ trait covariance in ecosystem responses to environmental change

4.1 INTRODUCTION

Of the many detrimental anthropogenic processes, land-use change is the greatest threat to global biodiversity (Sala et al. 2000, Foley et al. 2005) and therefore is likely to impose severe impacts on the structure and resilience of communities. As a result, numerous studies have investigated the impacts of different aspects of land-use change on biodiversity loss and compositional responses (Fleischner 1994, Turner 1996, Hansen et al. 2005). However, not all species exhibit the same responses to environmental stressors, and these responses can be strikingly context dependent, resulting in seemingly unpredictable changes in community structure following disturbances (Ewers and Didham 2006a). In an attempt to move beyond the apparent idiosyncrasies in community responses to land-use change, many studies have adopted a trait-based approach in order to better explain the variability observed in these community responses.

Many traits have been identified as important determinants of how specific species respond to environmental stressors, including morphological, behavioural, and life-history traits (Henle et al. 2004). Five species traits, in particular, have been suggested as the most important determinants of species response dynamics: trophic level, dispersal ability, body size, niche breadth, and rarity (Ewers and Didham 2006a). At the community level, the result is an ‘ecological filtering’ process, whereby the non-random loss of species that are particularly sensitive to disturbance alters the trait composition of communities (Webb et al. 2010). For example, Driscoll & Weir (2005) found that flightless beetle species (conferring poorer dispersal ability) were more susceptible to habitat fragmentation, resulting in proportionately higher numbers of winged beetles in agricultural habitats. Another study by Larsen et al. (2008) found that, following the fragmentation of continuous rainforest in Venezuela, large-bodied species that also had high dispersal ability were able to persist in the landscape, but only in low numbers among smaller fragments due to the large habitat area requirements associated with a large body size. If the trait composition of ecological communities is likely to change following anthropogenic land-use change, this change is also likely to have impacts on ecosystem functioning mediated by these communities.

Growing concern over adverse ecosystem responses to global environmental change has provoked extensive effort toward understanding the mechanistic determinants of the loss of associated ecosystem processes (Naeem and Wright 2003). From this work, significant advances have been made in understanding the causal and correlational links between biodiversity and ecosystem functioning (Huston 1997, van der Heijden et al. 1998, Loreau et al. 2001). Even though there has been considerable debate over the relative importance of qualitative (i.e. species identity) versus quantitative (i.e. species richness or absolute abundance) drivers of ecosystem function, species' traits have been identified as an undeniably important determinant of ecosystem processes (Chapin III et al. 2000, Larsen et al. 2005, Hillebrand and Matthiessen 2009, de Bello et al. 2010). Many studies have shown that knowledge of community structure and associated trait composition can accurately explain rates of ecosystem processes (Didham et al. 1996, Savage et al. 2007, de Bello et al. 2010). These findings point to the importance of measuring species' traits in studies attempting to quantify functional consequences of global environmental change.

A species' traits can have varying degrees of influence on the impact which that species has on its surrounding ecosystem. The vast body of literature supporting the relative effects of species traits on ecosystem functioning has predominantly focused on vascular plants (> 55%) and terrestrial invertebrates (> 20%), with an especially large focus on nutrient cycling processes (de Bello et al. 2010). For example, Garnier et al. (2004) demonstrated that a suite of plant leaf traits (specific leaf area, leaf dry matter content, and nitrogen concentration) determined variability in a number of ecosystem processes including primary productivity, decomposition rates, and levels of soil carbon and nitrogen. Furthermore, Orwin et al. (2010) found that relative growth rate of plants was an accurate predictor of leaf and litter quality, which in turn significantly affected microbial community composition and resulted in alteration of nutrient cycling rates. Other functional traits such as body size are also important determinants of ecosystem processes. For example, a study on aquatic invertebrate communities revealed a positive effect of detritivore body size on processing rates of leaf litter, whereas large-bodied invertebrate predators had a larger negative impact on the detritivores, thus negatively affecting leaf litter decomposition (Lecerf and Richardson 2011). Likewise, life-history traits are also important mediators of ecosystem processes, as demonstrated in a study by Norling et al. (2007), where bioturbation caused by burrowing benthic macroinvertebrate fauna influenced rates of organic matter mineralisation and oxygen uptake.

Several studies have been quick to point out that it may not only be variation in absolute trait means within a community that is important in ecosystem functioning, but also the degree of complementarity in traits across species (Loreau et al. 2001, Schumacher and Roscher 2009). Niche complementarity, or the asynchrony of species resource or habitat use due to trait variation among species (Hooper et al. 2005), can greatly increase rates of ecosystem processes as more species can exploit spatially or temporally heterogeneous resources. In other words, if a given resource is heterogeneous, specific traits may make some species better able than others to obtain the resource in different contexts, and an increase in trait variability across multiple species can lead to a community more fully exploiting that resource. For example, Striebel et al. (2009) found that light resources were finely partitioned between algal species that utilised different wavelengths of light, concluding that algal communities with higher species richness could more fully exploit available light resources, which resulted in higher biomass production and respiration. A similar pattern was found in a tropical plantation crop system whereby a greater diversity of pollinator body sizes increased the percentage of flowers that were pollinated due to varying dispersal abilities of insect pollinators (Klein et al. 2008). Niche complementarity can also be driven by the variation in behaviour between species. For example, Hoehn et al. (2008) demonstrated that when the vertical position of flowers were altered in pumpkin crops, a greater diversity of pollinator functional guilds provided higher rates of pollination due to an increased range of flying heights between different pollinators and behaviour within the flowers.

By measuring the trait composition of a community, there is a greater likelihood of detecting directional community responses to land-use change and, importantly, determining what these responses will entail for the functioning of ecosystems. This approach integrates the use of traits that determine variability in species responses to environmental change, and traits that explain variability in ecosystem process rates carried out by species, by identifying potential covariance between these ‘response’ and ‘effect’ traits. The incorporation of this so-called ‘response-effect trait framework’ (Lavorel and Garnier 2002) into ecological and conservation research has provided important insight into the impact of global environmental change on ecosystem functioning (Lavorel and Garnier 2002, Suding and Goldstein 2008). There are various possible scenarios of response and effect trait relationships, from negative covariance, to no relationship, or positive covariance between response and effect traits (Larsen et al. 2005). In a worst case scenario, positive covariance between response and effect traits may greatly exacerbate disturbance effects on ecosystem functioning, because traits that confer greater susceptibility to environmental change are also especially important for mediating rates of ecosystem processes (Larsen et al. 2005). In this case, species that are lost first following a disturbance are also the most functionally important, resulting in the rapid decay of ecosystem function.

Despite the importance of response-effect trait relationships, there has been little attention paid to their role in understanding trajectories of community reassembly in the restoration of degraded ecosystems. While it may be assumed that the same response traits that determine species loss from degraded habitats might also determine which species will become re-established in restored habitat, this may not always be the case. For example, species with low dispersal ability are more likely to be lost first as a result of habitat fragmentation (Larsen et al. 2008). However, species with higher dispersal power are more likely to naturally recolonise regenerating habitat from the surrounding landscape, which can result in a lag period before poorer dispersers recolonise these areas (Moir et al. 2005, Pywell et al. 2011). The way in which these structured responses will impact on ecosystem responses will depend on the covariance in response and effect traits of recolonising species.

In this study, I test the trait determinants of dung beetle community responses to edge effects in a heavily-degraded Nigerian montane forest and determine the shift in species and trait composition in response to habitat restoration in the surrounding land-use matrix. I then test the degree of covariance between response and effect traits, relating changes in trait distributions to variation in rates of dung removal following the removal of external anthropogenic threats. Although invertebrates are the second most represented taxa in studies investigating trait-mediated ecosystem processes, the trait determinants for this taxonomically diverse group are still poorly understood (de Bello et al. 2010). In particular, there are few studies that take into account multiple effect traits and measures of trait divergence that might explain complementarity effects (de Bello et al. 2010), despite the vast importance of invertebrates for ecosystem processes (Samways 1993). To identify the determinants of rates of beetle-mediated dung removal, I test the relative importance of three hypotheses for explaining variation in dung removal rates: neutral effects, trait-mean effects, and niche complementarity effects. First, in the ‘neutral effect’, I pose the hypothesis that species are functionally equal and that ecosystem processes (in this case dung removal rate) can be explained as a purely mass-dependent process (in this case variation in total dung beetle mass) within a given trophic level (Hubbell 2005). Second, in the ‘trait-mean effect’, I pose the hypothesis that over and above mass-dependent effects, trait-mean composition has a significant effect on relative rates of ecosystem function (de Bello et al. 2010). Third, in the ‘complementarity effect’ I pose the hypothesis that over and above mass-dependent effects, trait dispersion (or divergence in trait values within a community) has a significant effect on relative rates of ecosystem function, independent of variation in trait-mean composition across sites. By addressing these questions within the context of matrix restoration adjacent to forest edges, I aim to quantify the success of these restoration areas in conserving invertebrate communities and restoring crucial ecosystem processes.

4.2 METHODS

4.2.1 Study design

The study was conducted in Afromontane forest at the Ngel Nyaki forest reserve, located on the Mambilla Plateau near the south-eastern border of Nigeria (for a detailed description of the study site see Chapter 2). To quantify the impact of edge effects and matrix restoration on dung beetle community structure and associated beetle-mediated nutrient cycling processes, I sampled dung beetle communities and dung removal rates along three replicate forest-to-matrix edge gradients in both degraded and regenerating sites. Degraded sites were located in areas that were fully exposed to multiple anthropogenic threats (such as intensive cattle grazing and fires), compared to the regenerating sites that were located in areas where these threats were entirely excluded by fencing and restoration of the matrix surrounding forest edges. One additional ‘dummy edge gradient’ was placed in each of the deep forest and deep matrix habitats, at least 640 meters from the forest edge, to test for potential spatial autocorrelation in trap capture rates due to variation in trap spacing (Baker and Barmuta 2006). Each replicate edge gradient consisted of 13 sampling points at fixed distances from the edge on a doubling scale (-160, -80, -40, -20, -10, -5, 0, 5, 10, 20, 40, 80, and 160 meters from the edge, where negative values represent forest samples) (see Chapter 2 for full experimental design). Traps were laterally offset from one another, so that no two traps were closer than 50 meters apart in order to maintain independence between traps, as this distance is just beyond that which dung beetles can detect dung (Larsen and Forsyth 2005). This method of trap placement therefore controlled for potential sampling bias from trap interference and spatial autocorrelation (Baker and Barmuta 2006).

4.2.2 Sampling, sorting, and identification of dung beetles

All sampling of dung beetle communities was conducted at Ngel Nyaki forest during the late rainy season from October 4th to November 29th 2009. I used pig dung-baited pitfall traps (see Chapter 2 for trap design) placed at each distance across the edge gradient for two consecutive 24 hour periods (pooled 48 hour samples for each edge gradient transect) to ensure adequate sampling of the entire local community. All dung beetles in the subfamily Scarabaeinae were sorted to genus and assigned to initial ‘morphospecies’ groupings based on consistent morphological traits. Formal species identification was then undertaken by Rowan Emberson at the Lincoln University entomology collection and Frank Krell at the Denver Natural History Museum. For detailed sampling methods see Chapter 2.

4.2.3 Measurement of functional traits and dung beetle biomass

To quantify variation in functional trait composition between communities at regenerating and degraded edge gradients, five morphological traits were measured for individual dung beetle specimens within each species: body mass, body size, body condition index, wing area and wing loading. Body mass was calculated as the dry weight (mg) of each beetle, whereas body size was estimated from the width (mm) of the pronotum. From these measures, I calculated the ratio of body mass to body size which was used as a body condition index. Wing area was calculated as the total area of the left hind wing (mm^2), multiplied by two for total wing area, which was then used to calculate wing loading as the ratio of body mass to total wing area. To take into account within-species trait variation, I measured multiple individuals within each species for all samples collected. However, for species that were highly abundant, I used a randomised subsampling procedure so that at least 20 individuals were measured per sample for each abundant species. For a detailed description of functional trait measurement and the random subsampling technique, see Chapter 3.

For trap samples in which some individuals of abundant species were not sampled, I randomised the measured trait values from a given species in a given sample and then allocated these randomly-selected measurements to the remaining unmeasured beetles of that species. This assignment of randomly-selected measurements to remaining non-sampled specimens (rather than simply allocating a trait-mean to non-sampled specimens) maintained realistic levels of variability among individuals and allowed for accurate extrapolation of trait variability to the community level. In doing so, this method allowed for the scaling up of functional trait variation from the individual to community level, which can provide strong inference about response-effect trait relationships (Suding et al. 2008). In order to estimate the total biomass of dung beetles for each sample, I added the subsampled and estimated mass measurements from all specimens in a given sample.

4.2.4 Quantification of dung removal rates

To quantify the impact of edge effects and matrix restoration on dung removal rates, I placed experimental dung piles at all 101 sampling points and measured removal over a 24 hour period. Dung removal experiments were undertaken 1 – 2 days prior to baited pitfall trapping of dung beetles at each site, in order to avoid potential trap depletion effects on beetle communities that might otherwise have confounded dung removal rates. At each sampling point (as described above for pitfall trapping) a dung placement location was identified, avoiding visible large rock or logs that might bias burial behaviour by dung beetles (but always within 1 meter of where the pitfall trap was going to be located). Any debris such as dead wood or leaves within a 15 cm radius of dung placement was removed down to the topsoil and 40 g of fresh pig dung was placed directly on top of the bare soil.

All dung used for an entire site came from a single homogeneous batch of freshly-mixed dung (less than 12 hours old). In order to accurately determine the mass of dung removed by dung beetles, it was essential to know the initial and final moisture contents of the dung (which might vary between batches and also with environmental conditions in the field). Therefore, the 40 g samples of dung were weighed out from that day's homogeneous batch and wrapped individually in plastic bags in order to prevent desiccation of the dung (as well as inadvertent colonisation by insects) before placing in the field. At the same time, another fresh 40 g subsample from the same batch was also weighed out and placed directly in a drying oven at approximately 80 °C for at least 48 hours until constant dry mass was achieved, and this value used to determined batch moisture content. The experimental dung samples were left on the surface of the soil for 24 hours and then any remaining dung re-collected, being careful to avoid collecting any debris. In the laboratory, any invertebrates found in the remaining dung were carefully removed to avoid bias in dung mass loss estimates. The dung samples were then put into the drying oven in paper envelopes at approximately 80 °C for a minimum of 48 hours until a constant dry mass was achieved. To calculate the proportion dry mass of dung removed during the 24 hour period I used the formula:

Mass loss = (initial wet mass * (1 – initial batch moisture content)) – final dry mass

4.2.5 Statistical Analysis

4.2.5.1 *Using continuous response functions to quantify functional effects of matrix restoration*

Variation in the total capture rates of dung beetles and rates of dung removal were analyzed across forest-to-matrix gradients for each of the two levels of matrix restoration (degraded versus regenerating), using the statistical approach of Ewers & Didham (2006b). Using a form of the general logistic model, I determined the best-fit edge model out of five models of increasing complexity (Ewers and Didham 2006b). For specific methods on the model fitting procedure, see Chapter 2.

4.2.5.2 *A multilevel path model to disentangle causal pathways of functional responses*

To determine whether a correlation between beetle activity and dung removal was driven by purely neutral, mass-dependent, processes (i.e. total beetle mass irrespective of species identity) or by variation in the abundances of species with differing traits, I used a hierarchical SEM (structural equation modelling) approach in the R language environment. To test trait versus neutral effects in dung beetle-mediated nutrient cycling processes, I partitioned potential explanatory pathways into three main hypotheses (Figure 4.1). Firstly, rates of dung removal are entirely dependent on total dung beetle biomass. Secondly, dung removal rates are dependent on average trait values expressed in a given community and thirdly, there is a niche complementarity effect whereby community functional trait dispersion determines dung removal efficiency of dung beetle communities.

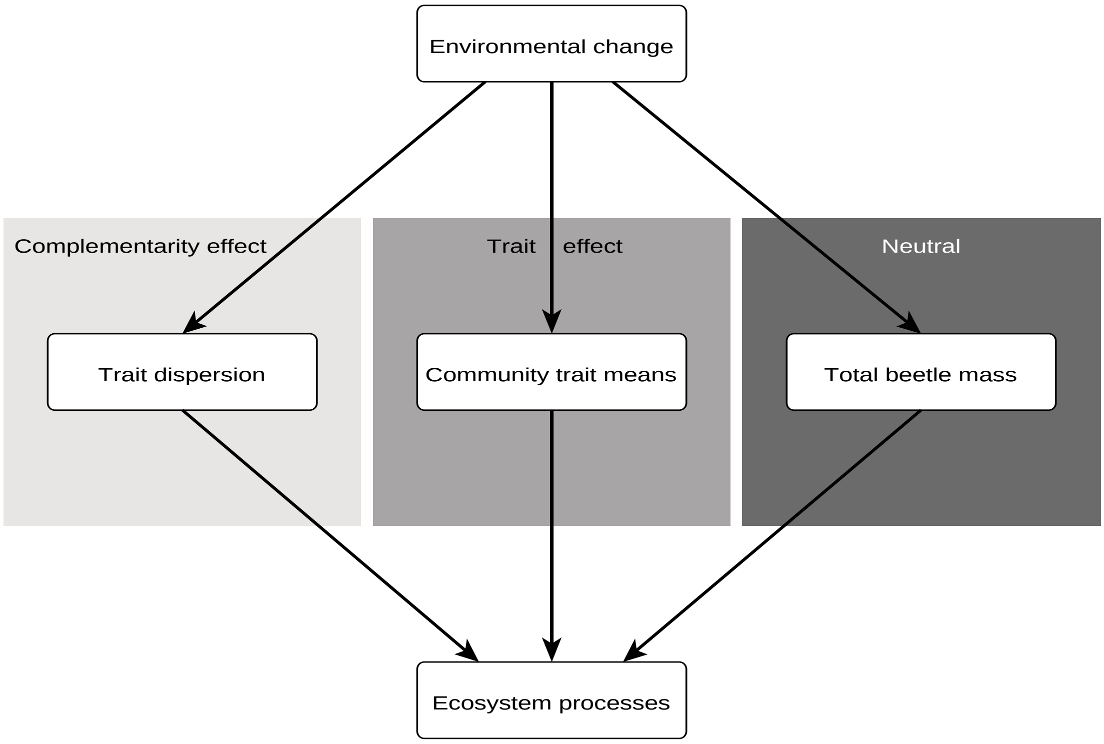


Figure 4.1 Hypothetical causal pathways of the effects of environmental change on insect mediated ecosystem processes. Shaded boxes indicate the causal hypotheses (neutral effect, trait-mean effect, or complementarity effect).

As a measure of functional trait complementarity, I calculated a distance-based metric of trait functional dispersion (FDis) using the “FD” package in the R language environment (Laliberte and Legendre 2010). The FDis metric takes into account multiple trait characteristics of organisms within a community and measures the distance of each species to the trait-mean centroid of the whole community. It is a multivariate adaptation of weighted mean absolute deviation from the trait centroid, where the weighting is given by the relative abundance of species (Laliberte and Legendre 2010). It is thus a weighted measure of trait variation or complementarity among species in a given community. To calculate FDis, I first compiled a trait matrix with mean trait values for each species, then calculated Gower dissimilarity coefficients among species trait complexes using the “gowdis” function. This was used to determine multivariate dispersion of assemblages based on the Gower dissimilarity coefficients weighted by species’ relative abundances.

Due to the hierarchical nature of the data, I used generalised multilevel path models, which are also highly flexible in dealing with non-linear data and interactions (Shipley 2009). To test the validity of a multilevel causal path model, several steps must be taken. Firstly, I identified the 'basis set' $\mathbf{B}_U$ of independence claims that are implied in a directed acyclic causal diagram (i.e. a unidirectional box-and-arrow diagram). $\mathbf{B}_U$ expresses the full set of independence claims (i.e. pairs of variables in the acyclic model with no arrow between them) and dependence claims (pairs of variables in the model with a causal arrow joining them). Secondly, I determined the probabilities p_i for each of the k independence claims in $\mathbf{B}_U$ using linear mixed effects models for normally-distributed response variables and generalised mixed effects models for binomially-distributed response variables. The combined p_i of the full model was calculated as $C = -2\sum_{i=1}^{k} \ln(p_i)$, and the C statistic was then compared to a chi-square (χ^2) distribution with $2k$ degrees of freedom (Shipley 2009). This gives the probability P that the model does not depart significantly from what would be expected under such a causal model (Shipley 2009). A model can be rejected if the P-value derived from the C statistic is smaller than the specified α-level (in this case $\alpha = 0.05$). Therefore, if $P > 0.05$ the causal model is not rejected and provides a good fit to the data.

Linear mixed effects models were fitted using the ‘nlme’ package and generalised mixed effects models were fitted using the ‘lme4’ package in R, with ‘transect’ (i.e. the three replicates of forest-to-matrix edge gradients in degraded versus regenerating matrix sites) specified as a random factor for all tests. Overdispersion in the generalised mixed effects models was taken into account using a poisson log-normal distribution whereby an observation-level vector is included as a random factor (Elston et al. 2001, Bolker et al. 2009). Assumptions of normality were tested for linear models by inspecting the variance structure of each model. For linear mixed effects models, distance from edge and mean dung beetle body mass were log-transformed to linearise relationships. All predictors in the model were mean-centred by subtracting the mean of a given variable from each value of that variable.

To fit the individual path coefficients that led to endogenous variables (measured variables within the model that have arrows leading to them) I used restricted maximum likelihood (REML) estimation and tested for their significance. As all predictors in the model were mean-centred, unstandardised path coefficients could be interpreted as the degree of change in the response variable for a given unit change in the predictor. However, interaction terms are interpreted differently whereby the coefficient indicates the amount of change in the slope of the regression of the response variable against a predictor following a unit change in the other interacting predictor variable (Aiken and West 1991).

I assessed model fit for all endogenous variables using an approximation to a R^2 statistic, calculated using a procedure developed for linear mixed effects models. The use of R^2 statistics in mixed effects models is under debate and the method used here assumes maximum likelihood (ML) estimation as opposed to REML, therefore the interpretation of my R^2 approximation should be judged with caution. Nevertheless, I believe that the statistical approximation provides a useful relative measure of fit of the model for the data used in the linear mixed effects models. For the binomial generalised mixed models, there is no appropriate approximation to R^2 statistics and the use of such a measure can be misleading. Therefore, as a pragmatic approach to provide a nominal estimate of the R^2 value for binomial models, I reanalysed using an arcsine square-root transformation of the response variable and carried out a linear mixed effects model followed by the R^2 method of approximation described above as a guide to assess the model fit (note that this approach was only applied to calculate an approximate R^2 value and was not used for calculating unstandardised path coefficients or other aspects of model fit).

Standardised path coefficients were calculated to assess relative predictive strength of each predictor on endogenous variables. This was done by taking the mean-centred values of each predictor and dividing each value by the standard deviation of the respective predictor. After rerunning the model with standardised variables, standardised path coefficients were interpreted in a similar way to the unstandardised coefficients, except that units of change are expressed in units of standard deviation. Therefore, standardised path coefficients can be directly compared between effects and thus indicate the relative importance of each path. However, this method of standardisation could not be used for binomial models (as the response is a column-bound ratio of proportions) and so the standardised path coefficients of binomial models were approximated using linear mixed effects models with an arcsine square-root transformation of proportion data.

4.3 RESULTS

4.3.1 Matrix regeneration alters beetle activity and associated ecosystem function

A total of 4705 dung beetles were captured across the entire sampling effort, comprising 36 species in 12 genera. Of these, 28% of species were captured exclusively in forest habitat and 42% were restricted to matrix habitats. There was a significant negative effect of distance from edge on the relative capture rates of dung beetles across forest-to-matrix gradients (Figure 4.2, Table 4.1). However, edge responses differed markedly between degraded and regenerating sites, with overall capture rates being significantly higher in regenerating sites (for samples collected on both sides of the forest edge) (Figure 4.2, Table 4.1). Although edge effect magnitude (or the range between forest and matrix asymptotes in total capture rates) was similar between degraded and regenerating edge gradients, there was greater spillover of beetles from the forest into the matrix at edges adjacent to regenerating matrix habitat (Figure 4.2).

Dung removal rates also varied dramatically across habitat edge gradients, ranging from an average of >75% dung removal over a 24 hour period in the forest interior to ~0% removal in the matrix habitat (Figure 4.2). The patterns of response in dung removal rates across edges and between degraded and regenerating matrix sites closely matched the patterns of variation observed for dung beetle capture rates (Figure 4.2). There was a large increase in rates of dung removal at forest sites adjacent to regenerating matrix with up to a 6 fold increase in dung removal compared to degraded forest sites (Figure 4.2). Of particular interest was the apparent off-site effects of adjacent matrix regeneration, as there were only significant increases in dung removal rates within the forest and not in the regenerating matrix itself (Table 4.2).

Table 4.1 AIC scores obtained from the edge function fitting procedure for models of increasing complexity (null, linear, exponential, logistic, and unimodal) for both regenerating and degraded edge gradients. AIC scores in bold indicate model of best fit for a given response.

Response	Null	Linear	Exponential	Logistic	Unimodal
Degraded matrix					
Capture rate	214.74	197.365	NA	**186.412**	243.325
Dung removal	-21.364	-26.628	NA	-26.09	**-30.489**
Regenerating matrix					
Capture rate	229.629	203.526	NA	**201.38**	256.617
Dung removal	35.256	**14.7**	NA	17.428	15.195

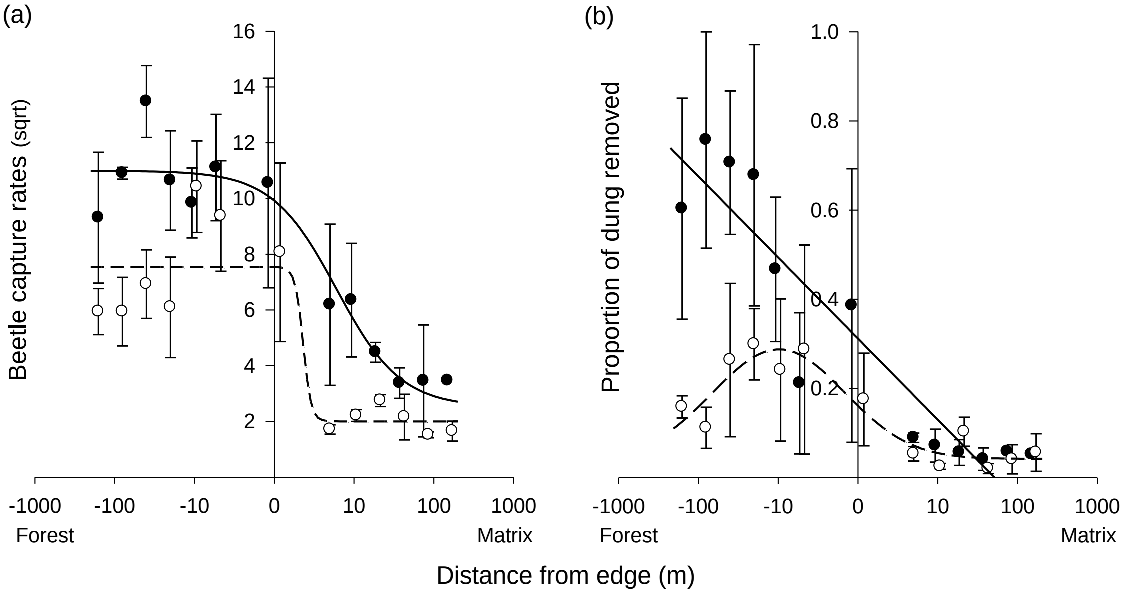


Figure 4.2 Variation in square root-transformed dung beetle capture rates (number of beetles captured per 48 hour trapping event) and proportion of dung removed (mean ± 1 SE) across degraded (open symbols and dashed fitted lines) versus regenerating (closed symbols and solid fitted lines) edge gradients. Negative values on the x-axis indicate forest sites. Lines are the best-fit continuous edge response functions of five fitted models of increasing complexity. Overlapping data points are offset for clarity.

4.3.2 Discriminating potential trait determinants of beetle mediated ecosystem processes

Results from the multilevel path analysis revealed that the strong correlation between beetle activity and dung removal rates could be attributed almost equally to both mass-dependent and trait-dependent effects. Total biomass of dung beetles decreased significantly from the forest to matrix habitat and was significantly higher in regenerating habitats. Interestingly, there was also a positive effect of mean body mass of dung beetle species on total beetle mass per sample (Figure 4.3). Trait composition also responded significantly to both habitat edges and matrix regeneration with an increase in mean body mass of individual species from the forest to matrix habitat (Figure 4.3). However, this positive effect interacted negatively with matrix restoration, thus reducing the intensity of edge responses in community-weighted trait distributions for both mean body mass and wing loading. Any potential effects of distance to edge and adjacent matrix restoration on the distribution of community-weighted BCI were fully explained by variation in mean body mass and so there was no direct effect of the main drivers on composition of community BCI. Likewise, there was no significant direct effect of matrix restoration or distance to edge on functional trait dispersion after controlling for community weighted body mass and wing loading.

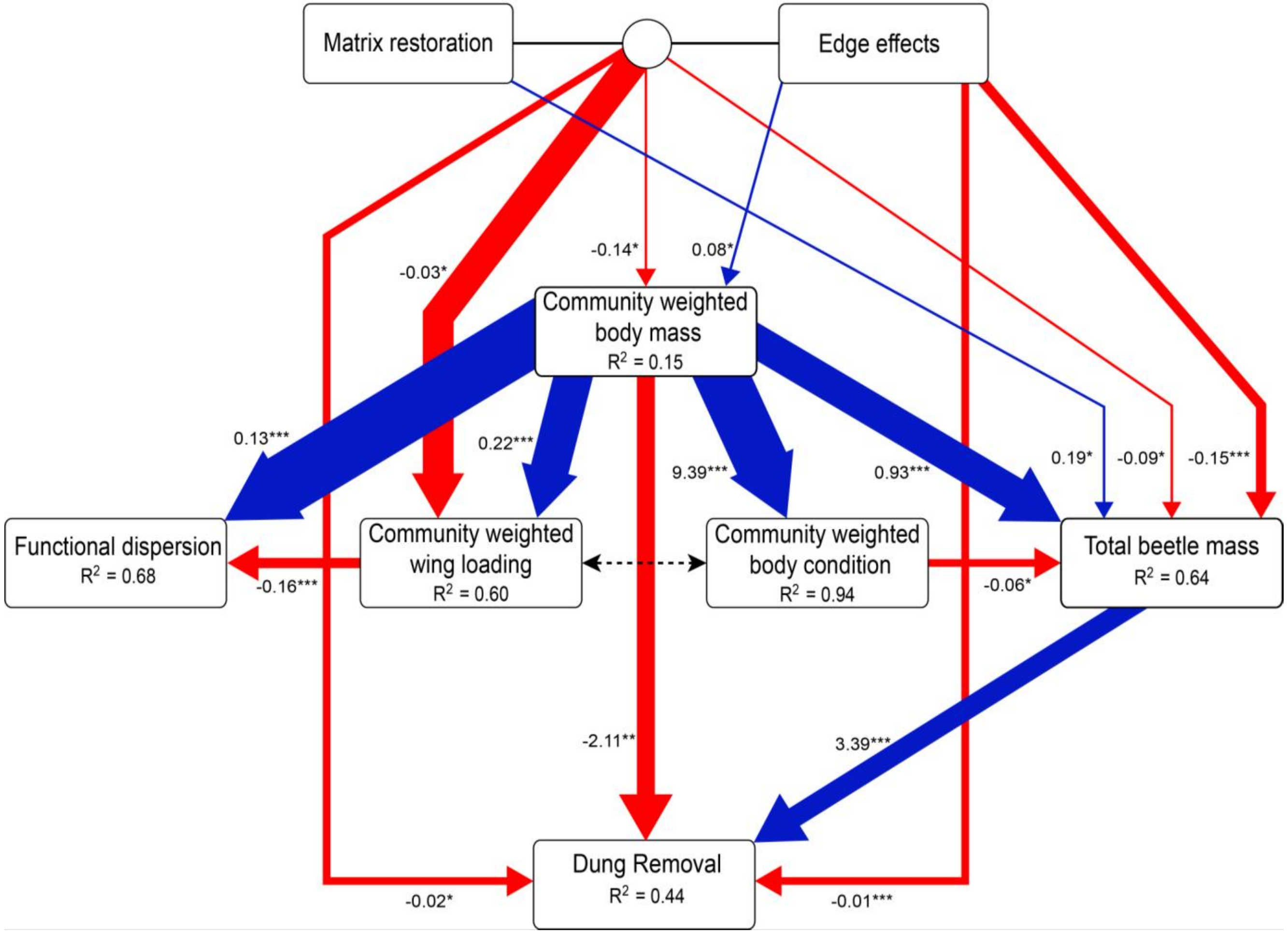


Figure 4.3 Directed acyclic diagram of generalised multilevel path analysis on causal pathways of functional responses to edge effects and adjacent matrix restoration using the best fit model (χ^2 = 19.981, df = 22, P = 0.584). Boxes depict predictor and response variables and arrows indicate significant positive (blue) and negative (red) effects. The circular node between 'matrix restoration' and 'edge effects' represents an interaction term and dashed arrows indicate collinear predictors. R^2 values in the endogenous variables are linear mixed model approximations to an R^2 statistic indicating the strength of fit for the model. Values adjacent to the lines are the unstandardised path coefficients with level of significance (*p < 0.05, ** p < 0.01, *** p < 0.001). Line weightings indicate the relative strength of effects, as derived from the standardised path coefficients.

There appeared to be no effect of community trait dispersion on rates of dung removal, despite the strong association of trait composition with dispersion. However, the path analysis revealed that community trait composition significantly affected dung removal rates. In particular, there was a significant negative effect of community weighted body mass on dung removal rates. This trait effect was evident even after controlling for total dung beetle biomass which was found to drive a positive response in rate of dung removal (Figure 4.3).

4.4 DISCUSSION

In landscapes under severe threat from anthropogenic land-use change, positive covariance of response and effect traits in invertebrate communities can potentially drive a rapid decline in ecosystem function in response to these threats. Results from this study demonstrate that dung beetle-mediated nutrient cycling rates respond strongly to edge effects as a result of a non-random shift in community trait composition and loss of total beetle mass. Moreover, there was a significant indirect effect of habitat edges on functional trait dispersion, mediated by the changes in community trait composition, although this appeared to have no effect on dung removal rates after taking into account community trait composition and total beetle mass. Interestingly, the restoration of the adjacent matrix habitat counteracted the strong effects of habitat edges in all cases, suggesting that simple restoration efforts may be highly effective in mitigating the detrimental effects of external anthropogenic threats on invertebrate communities and associated ecosystem processes.

4.4.1 Matrix restoration drives responses in total beetle mass and trait composition

Both total capture rates and total dung beetle mass decreased significantly with increasing distance from forest habitats into the adjacent matrix habitat, but this effect was ameliorated considerably in regenerating sites following matrix restoration. Interestingly, there was a positive effect of distance from the edge into the matrix on community-weighted mean body mass of dung beetles but this effect was reduced by matrix restoration. This means that, on average, there were larger beetles in the degraded matrix habitat. Curiously, there was a positive effect of community-weighted mean body mass on total beetle mass which is most likely a result of the strong effect that rare large beetles would have on small communities, especially in the matrix habitats. This result demonstrates the importance of large bodied invertebrates in heavily degraded ecosystems as they may partially compensate for biomass loss due to a decrease in overall abundances.

Community-weighted mean body mass was generally lower in regenerating matrix habitats. Many examples of animal responses to environmental stressors indicate that large bodied species tend to be more prone to extinction (Bennett and Owens 1997, Henle et al. 2004, Larsen et al. 2005) due to greater resource requirements, longer life-spans, and lower reproductive output. However, invertebrate body size is often positively correlated with physiological tolerances (Chown et al. 2002). Therefore, as this study sampled across continuous edge gradients which are analogous to gradients of environmental stress (Chen et al. 1999), greater physiological tolerances to factors such as temperature and humidity would likely be favoured in the degraded matrix habitat. Relative dispersal ability of species also responded strongly to environmental change, but it appears that the potential effects of habitat edges on community-weighted mean wing loading were very strongly counteracted by the restoration of the adjacent matrix habitat. As shown in other studies, dispersal ability is often stronger in species or individuals that are found in matrix habitats as they are better able to survive crossing hostile environments (Larsen et al. 2008, Meyer and Kalko 2008). Therefore, my results show that within landscapes subject to severe anthropogenic threats, dung beetles with low dispersal ability are more likely to persist in restoration areas undergoing regeneration. However, it is likely that the re-establishment of these smaller beetles may undergo a longer lag period as they are also less likely to recolonise restored habitat compared to highly mobile species (Moir et al. 2005, Tscharntke et al. 2005).

4.4.2 Neutral versus trait determinants of ecosystem process rates

Trait determinants of community responses to environmental change were also found to have a significant influence on rates of insect-mediated nutrient cycling. While I found no niche complementarity effect driven by variation in functional trait dispersion, there was a strong effect of community-weighted mean trait composition on dung removal rates, over and above neutral mass-dependent effects. These findings demonstrate that functional processes driven by dung beetles cannot be explained entirely by neutral effects that assume complete functional equivalence of species (Hubbell 2005). It is plausible that, irrespective of species diversity or the identity of individual species, a hypothetical community with only one species that is equal in total biomass to another community with multiple species, may potentially perform equal rates of ecosystem processes (Zhou and Zhang 2008). Results from this study show that, although purely mass-dependent effects accounted for 40% of the variation in dung removal rates, 34% of variation was explained by community-weighted trait mean composition, supporting the claim that neutral theory alone may not be able to fully explain functional processes (Chisholm and Pacala 2010).

Surprisingly, the strong mediating effect of community-weighted mean body mass on nutrient cycling was negative. This suggests that, in samples with a smaller weighted average body mass of dung beetle species, the removal rate of dung was proportionately greater per unit mass of beetles. Many previous studies have pointed to the importance of large dung beetles in nutrient cycling rates, whereby body size is assumed to be positively correlated with amount of dung sequestered (Klein 1989, Larsen et al. 2005, Nichols et al. 2008). However, previous studies have not quantified ‘gram for gram’ beetle-to-dung weight ratios of removal efficiency. As a result, my findings indicate that if total community biomass is held constant, communities composed of on-average smaller dung beetles are more likely to perform higher rates of dung removal. However, from these results one must bear in mind that community-weighted trait-mean body mass was also associated with an increase in overall total beetle mass and therefore still conferred an indirect positive effect on removal rates. This indicates the importance of large beetles in communities with low total beetle mass, where the presence of only one or two relatively large beetles may be integral to maintaining nutrient cycling when overall abundances of dung beetles are low in a given locale.

4.4.3 Functional trait dispersion reveals the strength of ecological filters

While there was no direct effect detected for matrix restoration and distance from forest edge on community trait dispersion, there were significant indirect effects of these drivers on functional trait dispersion via changes in community-weighted trait means. In particular, there was a highly-significant and powerful effect of community-weighted mean body mass on functional trait dispersion. This is most likely due to the rarity of larger-bodied beetles; 92% of captured dung beetles had a body mass of <10 mg, even though the total range of body mass across all beetles collected was from 0.45 to 1543.07 mg. Therefore, as communities appeared to consist of generally small-bodied beetles, the stochastic occurrence of a very large beetle could greatly increase the trait dispersion at that site. By contrast, there was a significant negative effect of community-weighted wing loading on functional dispersion (i.e. communities with low functional trait dispersion consisted of beetles with on-average higher community-weighted wing loading). A possible explanation is that communities that undergo strong ecological filtering processes (in this case edge effects and adjacent matrix condition) would be more likely to have beetles with higher dispersal ability, because poorer dispersers would be less likely to persist in these communities. This would have a very strong directional structuring effect, resulting in narrow and strongly-defined trait composition and therefore functional trait dispersion would be low.

These results have important implications for the need to quantify multiple traits, as measurement of single traits may fail to detect a response or could also give only a partial indication of responses in community trait composition. Additionally, by quantifying measures of trait range or divergence, in this case functional trait dispersion, it is possible to gain a clearer perspective of community filtering processes.

4.4.4 A response-effect trait approach explains functional outcomes of matrix restoration

Results from this experiment have shown that in forest surrounded by heavily degraded and disturbed matrix, the protection of the adjacent matrix can drive large increases in abundances of organisms and associated ecosystem processes, even after a very short period of time. Moreover, I found that the enhancement of dung removal rates is not just a function of beetle abundance or biomass. The ecological filtering of small-bodied dung beetles out of the dung beetle communities in open degraded habitats has led to assemblages with low total abundance and biomass of beetles, characterised by a few rare larger-bodied species, with low overall dung removal efficiency. As a result, degraded habitats are likely to undergo cascading changes in associated ecosystem functions including nutrient cycling rates and secondary seed dispersal that can have strong deterministic impacts on plant communities (Andresen 2003, Wu et al. 2011). The incorporation of a response-effect trait framework in this study provided useful insight into the mechanistic determinants of community reassembly and the following re-establishment of beetle-mediated ecosystem processes. In particular, this was demonstrated by a community shift to high total beetle mass composed of many smaller beetles, resulting in significantly higher rates of dung removal compared to degraded sites, a clear example of the effects of response-effect trait positive covariance (Larsen et al. 2005, Suding et al. 2008).

In conclusion, while there was a significant shift in species trait distributions and resulting beetle-mediated dung removal rates in response to edge effects, this was counteracted by the restoration of matrix habitat adjacent to habitat edges. As such, I propose that further research into community reassembly in restored habitats should test for potential cascading effects on ecosystem processes via community traits. By doing so, the qualitative versus quantitative drivers of ecosystem processes can be placed into context in systems recovering from anthropogenic land-use change. This study illustrates how an understanding of the direct and indirect effects of global change drivers on communities can shed light on the relative ecosystem benefits of habitat restoration efforts. This also presents great promise for simple restoration measures such as the exclusion of livestock and frequent fire disturbance in re-establishing invertebrate mediated ecosystem functioning in forest remnants.

Chapter 5: Discussion

5.1 Overview

There is virtually no ecosystem which remains unaltered by human impacts (Vitousek et al. 1997). Land-use change has been identified as the most important driver of biodiversity loss (Sala et al. 2000, Foley et al. 2005), and leads to the introduction and intensification of edge effects, which are potentially the greatest driver of ecosystem change resulting from habitat fragmentation (Ewers et al. 2007, Banks-Leite et al. 2010). Even in very large natural remnants, the spillover of anthropogenic edge effects can be pervasive and alter the structure and function of communities (Ewers and Didham 2008). These effects are trans-boundary phenomena being the product of the contrast between patch and matrix habitats (Fonseca and Joner 2007). Therefore, the structure of the matrix adjacent to a habitat patch is likely to be a strong determinant of the extent and magnitude of these effects. While the off-site impacts of matrix structure on within-patch dynamics have been addressed in the literature, almost no attention has been paid to the influence of anthropogenic land-use intensity in the adjacent matrix on the strength of edge effects (but see Piessens et al. 2006, Pawson et al. 2008). Moreover, there have been no studies that have quantified the relative off-site impacts of habitat restoration in the adjacent matrix on the reassembly of associated communities. In this study I tested for the influence of external anthropogenic threats in the adjacent matrix on within-patch ecosystem dynamics across habitat edge gradients. I quantified responses in dung beetle community structure by comparing abundances, species richness, and community composition to determine overall community patterns and also identify potential variation between species in their responses.

Species responses to anthropogenic drivers of change such as edge effects are often highly variable and can seem unpredictable. However, this variability is inherently non-random as species responses are strongly dependent on their morphological, life-history, and behavioural traits (Ewers and Didham 2006a). Certain traits confer different levels of susceptibility to environmental change, and can be used to predict species responses to environmental change (Henle et al. 2004). This provides great promise for understanding how communities will respond following a disturbance. However, few studies take into account phenotypic variation within species, which can mask trait effects or result in unexplained variability of trait-determined responses (Webb et al. 2010). In an attempt to provide insight into the importance of individual trait variability, I demonstrated how species exhibit variability across edge gradients between individuals and also among species by quantifying individual trait measures for entire communities across ecological gradients.

Species traits confer varying levels of susceptibility to disturbances but can also be responsible for determining the degree of influence that an organism has on its surrounding habitat (de Bello et al. 2010). These traits are important for understanding the proportional influence of particular organisms in mediating ecosystem processes and therefore can explain variation in functional efficiency between communities. In many cases, there can be overlap of response and effect traits (Suding and Goldstein 2008), where a trait that confers the level of susceptibility of a species to environmental change also determines the functional efficiency of that species. Such overlap can have serious implications for the functional resilience of communities, resulting in unexpected alteration of ecosystem function following environmental change (Larsen et al. 2005). By quantifying the effects of multiple drivers on community structure and relative changes in trait composition, I tested for potential covariance in response and effect traits to look for potential cascading impacts of edge effects and matrix restoration on dung beetle-mediated ecosystem processes.

5.2 Matrix restoration mitigates edge effects in dung beetle communities

Results from this study have shown that dung beetle communities responded dramatically to edge effects with a very large change in total abundances and marked differences in community composition across the habitat edge. Almost all species tested individually responded negatively to edge effects, although a few species were found to be edge specialists with especially high abundance around the edge habitat. This is arguably the strongest evidence found for dung beetle responses to edge effects. The clarity and predictive nature of these results were achieved by using continuous edge response functions across adjoining forest-to-matrix habitats and also by comparing edge effect strengths in a heavily degraded anthropogenic landscape. In contrast, previous studies on dung beetle responses to edges have either used categorical (habitat, edge, and matrix) sampling techniques (Spector and Ayzama 2003), not sampled into the adjacent matrix (Davis et al. 2001), and/or have only sampled across natural ecotones (Duraes et al. 2005). Therefore, bearing in mind the results of this study, it is imperative that research into community responses of dung beetles to habitat fragmentation incorporates more predictive methods for detecting edge effects in dung beetle communities.

While some studies have proclaimed the importance of the matrix habitat structure on within-patch community dynamics (Kupfer et al. 2006), almost no studies have explicitly tested the influence of adjacent land-use intensity in the matrix on edge effects (but see Piessens et al. 2006, Pawson et al. 2008). My research has shown that by comparing edge responses in dung beetle communities in forest habitat adjacent to heavily-degraded matrix and regenerating matrix habitat, edge responses can change dramatically as a result of matrix restoration. For example, between habitats adjacent to degraded and regenerating matrix, I found large increases in overall abundances and significant changes in community composition across forest-to-matrix edge gradients. Such a disparity in edge responses between degraded and regenerating habitats indicates the importance of taking into account the impacts of external anthropogenic threats when quantifying within-patch dynamics.

Among many factors, habitat size and landscape structure are often identified as important for maintaining the ecological integrity of ecological reserves (Collinge and Palmer 2002, Lindenmayer et al. 2006). In particular, habitat size effects may be due to the intercorrelated effects of habitat edges, which penetrate further in smaller habitat fragments, reducing their effective ‘core’ habitat (Laurance and Yensen 1991, Ewers et al. 2007). My findings suggest that another important consideration should be the influence of adjacent matrix habitat on the strength of edge effects. As adjacent matrix degradation can have such a strong mediating influence on the pervasiveness of edge effects, this is clear evidence that ecological reserves should take into account the potential interactions between these drivers of change. Ecological assessments of the effectiveness of conservation reserves should also quantify the impacts of the landscape context to gain more accurate estimations of minimum reserve size requirements.

The implications of my research can also be examined in another light, where adjacent matrix restoration can have significant conservation benefits for communities within habitat remnants. The implementation of restoration buffer zones of regenerating matrix habitat adjacent to forest systems has been suggested as an effective strategy for minimising external anthropogenic threats to remnant ecosystems (Gascon et al. 2000). While buffer zones of regenerating vegetation around forest edges have been shown to reduce the effects of adjacent matrix structure on within-patch dynamics (Denyer et al. 2006), no explicit evidence exists for its effectiveness as a means of alleviating edge effects. The large disparity in dung beetle community responses between forest-to-degraded matrix and forest-to-regenerating matrix across continuous edge gradients found in my study exemplifies the importance of protecting and restoring zones of matrix habitat surrounding ecological reserves.

5.3 Ecological filtering and the trait determinants of species responses

Significant changes in community composition indicated that there were large changes in the relative abundances of species and thus, species must be responding differentially to edge effects. By teasing apart individual species responses, I was able to reveal striking variability in the response functions and sensitivity of different species to edge effects and external anthropogenic threats. This leads to an important conclusion: all species are not equal in their sensitivity to environmental change, thus inferring that there must be mechanisms mediating these differences in species responses and overall community structure.

Much of the variability in species responses to environmental change stems from variation in morphological, behavioural, and life-history traits (Ewers and Didham 2006a). As a result, there has been considerable research invested into identifying functional traits that mediate the relative extinction proneness of different species under varying global change scenarios (Henle et al. 2004). Most studies have adopted a fixed-trait perspective whereby overall species trait values are used to predict the distribution or degree of a species' response (Driscoll and Weir 2005, Gibb et al. 2006, Lebrija-Trejos et al. 2010, Williams et al. 2010). However, this perspective fails to take into account the importance of individual-level phenotypic variation within species. This is despite potentially high phenotypic variability, trait plasticity, and even rapid evolutionary change in some populations subjected to intense anthropogenic stressors (Carroll et al. 2007, Hendry et al. 2008).

Findings from my research showed that certain species did respond differently to environmental changes, and that these responses were dependent on specific functional traits. This conclusion was reached by using the absolute mean of each measured morphological trait for a given species to predict the relative distribution between degraded and regenerating habitat edge gradients. Interestingly, these results showed that wing loading and body condition could explain species' sensitivities to heavily degraded habitat edges. However, to gain a more realistic understanding of how functional traits determined species distributions, I took into account all individuals and plotted total community trait means across degraded and regenerating edge gradients. This provided remarkable insight into habitat edge-associated gradients of ecological filtering processes, wherein there were significant changes in the distributions of all morphological traits across habitat edge gradients and between degraded and regenerating sites.

To determine the factors contributing to this non-random trait variability, I also demonstrated that individuals within species undergo ecological filtering, resulting in often non-random variability within species across environmental gradients. For example, 69% of species in this study were found to exhibit non-random trait variation across habitat edge gradients. As such, these findings suggest that due to within-species phenotypic variation across environmental gradients and changes in the relative abundances of species, community trait composition may vary quite differently than expected. Studies that do not adopt an approach that incorporates phenotypic variability into community-wide inferences are therefore likely to make inaccurate conclusions on the trait determinants of community structuring. For the future development of trait-based ecology, there needs to be a stronger focus on trait variability across individuals, not just across species (Webb et al. 2010). Additionally, trait plasticity may be highly important for masking or intensifying trait-determined community responses, indicating the need to better understand what role plastic responses of individuals play in community responses to global environmental change (Callaway et al. 2003).

In most cases, restoration efforts are aimed at re-establishing species assemblages that resemble those that would have been lost from the historical pristine habitat (Hobbs and Norton 1996). This study demonstrates that the presence of particular species may not necessarily confer a particular expected trait value for a species due to potential shifts in within-species phenotypic variability in response to varying levels of environmental stressors. Therefore, there may be significant disparity in trait composition between communities undergoing different environmental stressors, even if species composition is the same. In light of these findings, restoration efforts should consider the re-establishment of not only species assemblages, but also trait composition in regenerating communities. This lends further support to the idea that, even if the species components are reintroduced into a degraded ecosystem, this does not necessarily mean that the restoration attempt has been fully successful (Hobbs and Norton 1996). To better understand the restoration success of an ecosystem, it is important to also take into account the functional performance of re-established species assemblages (Benayas et al. 2009).

5.4 Community reassembly and the restoration of ecosystem functioning

Ecological filters, such as edge effects, have widespread impacts on the distribution of species traits by removing species with response traits that confer higher levels of susceptibility to environmental change. In the wake of this non-random species loss, the processes that are mediated by particularly sensitive species are also lost (Larsen et al. 2005). Therefore, the application of a response-effect trait framework is required to better understand the functional consequences of anthropogenically driven environmental change (Lavorel and Garnier 2002).

By testing the causal pathways through which edge effects and matrix restoration alter insect-mediated ecosystem processes, I was able to discriminate the mechanisms that mediated functional responses in dung beetle communities. I found that total beetle mass and community trait composition significantly responded to edge effects but these effects were counteracted by the restoration of the adjacent matrix. Despite the expected positive effect of total beetle mass on dung removal rates, there was a surprising negative effect of community-weighted mean body mass on rates of dung removal. This seemingly counterintuitive finding highlights the relative importance of disentangling determinants of ecosystem processes. Previous findings have always pointed to the functional importance of large dung beetles for dung removal (Klein 1989, Larsen et al. 2005, Nichols et al. 2008), however, my findings suggest that large assemblages of on-average smaller beetles may in fact be more important for maintaining high rates of beetle-mediated nutrient cycling. Bearing this in mind for studies quantifying the determinants of functional responses to environmental change, future research will benefit from using methods that can rigorously partition the relative importance of mediating factors. In doing so, more accurate and predictive inferences can be made for discriminating deterministic processes of ecological change under various global change scenarios.

Additionally, to my knowledge there are no studies that have investigated the off-site impacts of matrix restoration adjacent to remnant habitats on response and effect trait covariance and the importance for ecosystem function. Non-random community reassembly, as demonstrated here in dung beetle communities, appears to result in large increases in dung removal rates as these communities are re-colonised by small, highly abundant beetles. These results demonstrate that simple measures taken to restore adjacent areas of matrix habitat around forest reserves may be successful in rapidly re-establishing high rates of insect-mediated ecosystem function.

5.5 General conclusions

The investigation of dung beetle community responses to edge effects and matrix restoration has provided new insight into the potential off-site impacts that matrix degradation can have on within-patch ecosystem dynamics. Beyond quantifying the impact of these trans-boundary effects on dung beetle species assemblages and total abundances, I was able to identify the trait-based mechanisms driving these responses. However, a somewhat unexpected finding was the very high and non-random individual trait variation, leading to greater complexity than perhaps originally anticipated. These complex differences in individual traits were found to scale up to strong overall community responses in trait distributions which in turn had important flow-on effects to ecosystem processes. Perhaps the most striking conclusion from this research is that simple exclusion of anthropogenic threats from small areas of adjacent matrix can lead to a rapid and large response in community structure of dung beetles, resulting in the successful re-establishment of ecosystem processes. Therefore, this study has positive and important implications for future attempts to protect and restore ecological reserves using simple and affordable measures.

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